

THE EVOLUTION OF MUTUALISM AND OTHER FORMS OF HARMONY AT VARIOUS LEVELS OF BIOLOGICAL ORGANIZATION*

Egbert Giles LEIGH, Jr. ⁽¹⁾ & Thelma Elizabeth ROWELL, ⁽²⁾

⁽¹⁾Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Panama

⁽²⁾Department of Integrative Biology, University of California, Berkeley, California, USA

SUMMARY

(review paper)

At crucial stages in evolution, such as the origin of eukaryotes, metazoans and social groups, individuals benefitted by cooperating, and formed larger wholes. Mutualism is also pivotal in modern ecosystems. When can mutualism evolve ? Selection on individuals favors their group if, as for organelles grouped in host cells, groups exchange no migrants, each group has one parent group, and there are many more groups than individuals per group. Group members also cooperate if: 1. harming their group harms them, as in animals which need ALL members' help to avoid predators, or 2. other members can and will prevent acts which harm the group. A honeybee worker serves her colony rather than laying eggs, since most of her comrades are half sisters more related to the queen's young than hers, who eat any of her eggs they find.

KEY WORDS : Selection - Macroevolution - Symbiosis - Hierarchies - Ecosystems.

RÉSUMÉ

(article de synthèse)

L'ÉVOLUTION DU MUTUALISME ET DES AUTRES FORMES DE RELATIONS HARMONIEUSES ENTRE ESPÈCES À DIFFÉRENTS NIVEAUX DANS L'ORGANISATION DU VIVANT

À certaines périodes critiques de l'évolution – notamment celles qui concernent l'origine des eucaryotes, l'apparition des métazoaires et des groupes sociaux – les individus ont obtenu des avantages en coopérant. Ils ont alors eu tendance à former de plus grands ensembles et le mutualisme reste un pilier du fonctionnement des écosystèmes actuels. Dans quelles circonstances le mutualisme peut-il évoluer ? Les facteurs de sélection qui jouent sur les individus favorisent leur groupe si, comme dans le cas des organites d'une cellule-hôte, les groupes n'échangent pas de migrants, tous les individus d'un groupe ont le même groupe parental et si le nombre d'individus par groupe est nettement inférieur au nombre de groupes. Les membres d'un groupe tendent également à coopérer si (1) tout dommage fait au groupe est dommageable pour l'individu, comme dans le cas où des animaux ont besoin de l'aide de tous les membres du groupe pour éviter les prédateurs, ou (2) les autres membres du groupe ont la possibilité de s'opposer à ce qui est dommageable au groupe et agissent en conséquence. Une abeille se rend utile à son groupe en tant qu'ouvrière plutôt qu'en pondant des œufs qui seraient mangés par ses congénères, parce que celles-ci sont en fait des demi-sœurs plus proches des descendants de la reine que ne le seraient ses propres descendants.

MOTS CLÉS : Sélection - Macroévolution - Symbiose - Hiérarchie - Écosystèmes.

INTRODUCTION

Does natural selection imply an unrestrained competition which leaves no place for mutualism or cooperation? Is evidence for mutualism evidence against evolution by natural selection?

Darwin did not think so. When he was writing, the ideas of Adam SMITH were "in the air." Adam SMITH viewed competition as the engine which drives the development and maintenance of the complex mutualisms underlying human civilization. DARWIN noticed the mutualistic aspects of ecosystems (DARWIN 1859, THOMPSON 1994), and did not consider them evidence against his theory.

To learn when natural selection favors mutualism, and what rôle mutualism plays in evolution, I will pose three questions:

- 1) How has selection for harmony helped to shape the evolution of life on earth?
- 2) Under what circumstances will natural selection favor the evolution of harmony - benevolent, "neighborly" interactions, or, better yet, co-operation- among a group's members?
- 3) What are some of the ecological consequences of selection for harmony?

I will begin by explaining why I think these questions matter. I will then outline some major episodes in the evolution of life where natural selection for harmony played an unquestionable rôle. Next, I will describe some circumstances which allow the evolution of harmony. Finally, I will consider how mutualisms shape modern ecosystems. I will *not* try to assess the relative importance of mutualism and selfish exploitation in shaping modern ecosystems.

THE EVOLUTION OF HARMONY AND THE ORIGIN OF COMPLEXITY

HIERARCHY THEORY AND MAKING COMPLEX WHOLE FROM SIMPLER PARTS

To show why these questions matter, I will start from the one idea in "hierarchy theory" which I think captures a genuine and important truth: the virtue of making larger wholes by combining "ready-made" parts. This idea is embodied in KOESTLER's (1967) parable of two watchmakers. One, which he called Bios, started each watch by making sub-assemblies of ten basic parts apiece, then forming assemblies of ten sub-assemblies apiece, and so forth, until he had a finished watch. His counterpart Mekhos constructed watches basic part by basic part,

without benefit of intermediate sub-assemblies. Both watchmakers were subject to interruptions, which undid the structures which they were currently assembling. An interruption cost Bios no more than the ten steps of this current level of assembly, while his counterpart Mekhos could lose as many steps as there are basic parts in a watch. As interruptions are a fact of life, only Bios could finish any watches.

This parable has many reflections in biology. FISHER (1930) argued that the more complex is a structure, the less likely it is to be improved by a random change in it. As LEWONTIN (1978, p. 230) remarked, there must accordingly be some degree of independence between the effects of different genes, else the entity affected by a mutation would be so complex that the chance of a random mutation effecting an improvement in it would be too slight to provide the new favorable variants required to fuel continued evolution. In other words, mutations are more likely to be favorable if the organism is constructed as a set of quasi-independent modules.

Another, more fundamental, application of the same principle is that, to build complicated wholes, it is best to start with a reasonably trustworthy set of self-contained, ready-made parts. The biological counterpart of this principle is that the most spectacular increases in organismic complexity have arisen by combining collections of pre-existing individuals into larger, more complicated, but harmonious, wholes (MAYNARD SMITH and SZATHMARY 1995).

SELECTION AMONG GROUPS AND TURNING PARASITES INTO ORGANELLES

Eukaryotic cells evolved by combining parts to form more elaborate wholes. The mitochondria, chloroplasts, and cilia of eukaryotic cells, and perhaps even the spindle apparatus that makes mitosis and meiosis possible for eukaryotes, apparently descend from micro-organisms which either invaded ancestral eukaryotes or were "eaten" by them (MARGULIS 1981, MARGULIS and SAGAN 1986). Most of these organelles possess their own DNA or RNA, in which resides the primary evidence of their ancestors' existence as independent organisms (GRAY 1983, MARGULIS & SAGAN 1986). In short, eukaryotes evolved through a series of invasions by different endosymbionts, which the ancestors of eukaryotes eventually incorporated as essential features of their structure. Indeed, it was logical for eukaryotes to evolve thus. As DYSON (1985, pp. 12-13) put it:

"A living cell, in order to survive, must be intensely conservative. It must have a finely tuned molecular organization and it must have efficient mechanisms for destroying

promptly any molecules which depart from the overall plan. Any new structure arising within this environment must be an insult to the integrity of the cell. Almost by definition a new structure will be a disease which the cell will do its best to resist. It is possible to imagine new structures arising internally within the cell and escaping its control, like a cancer growing in a higher organism. But it is much easier to imagine new structures coming in from the outside like infectious bacteria, already prepared by the rigours of independent living to defend themselves against the cell's efforts to destroy them."

How could a common interest in the good of their cell evolve among so promiscuous a mix of quondam parasites? In general, intracellular parasites face an evolutionary choice between making "permanent" territories of the cells they invade, or using them as disposable springboards for infecting other cells. Which alternative is chosen depends on how rapidly the prospects of finding new hosts increase with increase of virulence and its attendant risk to the current host (MAY & ANDERSON 1983, 1990). If an initially virulent parasite infects every available host, however, the lack of new hosts favors "caring for" currently occupied hosts, just as the lack of more new land to colonize favors farmers who can cultivate their current holdings sustainably (NETTING 1990). The ancestors of organelles eventually made territories of their host cells, from which they excluded would-be immigrants. Nowadays, this territoriality is reflected at fertilization, when the few organelles carried in by the sperm are usually destroyed by their more numerous counterparts within the egg (EBERHARD 1980).

The conflicts of interest which do occur between organelles and their host cells, and the means by which they are suppressed (EBERHARD 1980), suggest how a common interest has evolved between these organelles and their hosts. Conflicts arise either because different organellar genotypes compete within a cell by means inimical to that cell, or because there is a conflict of interest between nuclear and organellar genes (EBERHARD 1980). Intracellular competition between organelles usually injures their cell for the same reason that competition between different parasite genotypes within a host favors increased virulence, injurious to the host (Bremermann & PICKERING 1983, MAY and ANDERSON 1990, HURST 1990). Conflict of interest between organelles and nuclear genes is reflected by cytoplasmic mutants which favor all-female sex ratios because females, unlike males, pass cytoplasmic organelles to their offspring (EBERHARD 1980, COSMIDES & TOOBY 1981, HURST 1992, 1993), and nuclear genes which suppress

cytoplasmic sex ratio distortion because males and females contribute equally to the nuclear genomes of the next generation (FISHER 1930).

Conflicts of interest between host cells and an invading species of endosymbionts can be suppressed by minimizing genetic variance among the symbionts within a host, and linking the symbionts' reproduction indissolubly to that of their hosts. By making territories of their host cells, ancestral organelles set the stage for both developments. Selection among sexually reproducing hosts favors inequality between egg and sperm when such "anisogamy" spares zygotes the inconveniences of a protracted combat between paternal and maternal organelles (COSMIDES & TOOBY 1981). Such anisogamy is the rule among animals, where an egg carries orders of magnitude more mitochondria than the sperm which fertilizes it (BIRKY 1991, p. 113). Where organellar territoriality enforces uniparental transmission of organelles, there is almost no genetic variation among the 100 to 10 000 organelles of a given type which live in each of an organism's cells (BIRKY 1991). Most animals, plants and fungi inherit organelles from the mother -although conifers inherit chloroplasts paternally (BIRKY 1991, CLEGG *et al.* 1991). In many species of single-celled organisms, one parent provides the organelles when sexual reproduction occurs, although when yeasts mate, their mitochondria fuse (BIRKY 1991). Minimizing genetic variance among the organelles of a given type within a host was a crucial step. The inescapable conflict of interest between organelles, which only reproduce through females, and nuclear genes, which favor devoting equal effort to each sex (COSMIDES & TOOBY 1981), creates a contest between cytoplasmic sex-ratio distorters and nuclear suppressors analogous to the "gene-for-gene" contests between infective rusts and resistant flax or wheat (BURDON 1987). In most species, however, lack of genetic variation among organelles enables the nuclear genes' interest in an even sex ratio to prevail- saving these species from extinction.

The subordination of selection among a protist's organelles to selection among the protists which carry them is a case where selection among populations overrides selection among the individuals within a population. The effectiveness of selection on a population of entities, whether these entities be organisms, or populations of organisms, depends jointly on the selection's intensity -the proportionate impact on an entity's reproductive success of a unit change in the characteristic under selection, and the genetic variance among this population's entities in the selected characteristic. Selection among populations is more likely to override selection within populations the higher the genetic variance among, relative to that within, populations (LEIGH 1983). This ratio is highest when there

is no exchange of migrants between populations, each population descends from a single pre-existing population, and there are many more populations than individuals per population (see Appendix, §4). The predisposition of the invading ancestors of modern organelles to make territories of the cells they occupied, led to their subjection to a group selection (each group being the inmates of a cell) so effective that a modern "eukaryotic cell can be likened to a society of a nucleus and a crowd of subcellular organelles in which all members co-operate for the common good." (EBERHARD 1980, p. 231). Indeed, it is astonishing that subcellular organelles descend from independent organisms, so perfectly are these organelles designed to serve the cells to which they belong.

Parasites have transformed into symbionts in the laboratory. A laboratory strain of amoebas became infected by rod-shaped bacteria, with between 60,000 and 150,000 living in each amoeba. At first, these bacteria killed most of the amoebae they infected, and greatly slowed the growth rate of survivors. These bacteria appeared to be obligatory parasites: they would not grow on any medium save the amoebae (JEON 1972). The infected population, however, did not die out, and was maintained for many years. Five years after the infection appeared, amoebae were carrying as many bacteria per cell as before, but they now grew and multiplied as fast as normal amoebae (JEON 1972, 1987). Moreover, these amoebae could not survive if their bacteria were removed, while their bacteria were no longer dangerous to "naïve" amoebae (JEON 1972, 1987, JEON & AHN 1978).

SEXUAL REPRODUCTION, GROUP SELECTION, AND MULTICELLULAR ORGANISMS

Sexual reproduction played a major rôle in aligning the advantage of individual cells in a multicellular organism with the good of their organism. Indeed, the evolution of multicellular organisms hinged upon the production of one-celled zygotes by sexual reproduction, and the mitotic division of these zygotes to form organisms whose cells were genetically identical, save for mutational error (MAYNARD SMITH 1988). Since each zygote is genetically unique, while the cells of the organism that grows from it are genetically nearly identical, selection among organisms overrides selection among cells within organisms (Maynard Smith 1988). Nowadays, where there is risk that cells may migrate from one individual to another, defenses such as histoincompatibility systems have evolved to prevent it (BUSS 1987), as if it were important to preserve the genetic uniqueness and homogeneity of individuals.

Multicellular organisms have developed defenses against selfish cell lineages, such as cancers, which arise by somatic mutation and spread in ways which injure their organism. In animals, such defenses include sequestration

of the germ line (to prevent mutant lineages from invading it to further their own reproduction) and maternal control of the early stages of development (to minimize damage from a selfish lineage). In plants, rigid cell walls prevent the metastasis of selfish cell lineages throughout the organism (BUSS 1987). These defenses, however, presumably evolved only because evolution among organisms routinely overrode selection among cells within organisms.

An organism's "choice" of defense against selfish cell lineages involved tradeoffs which distinguish whole kingdoms of life. For example, the rigid cell walls of plants prevent sequestration of the germ line. Thus plants, which can reproduce by cloning or fragmentation, are less individual than flies, snails or squirrels, so theorists tie themselves in useless knots over whether morphological individuals (ramets) or clones (genets) are the units of evolution.

THE EVOLUTION OF COOPERATION AND THE ORIGIN OF LIFE

Evolving harmony among different components appears to have played an essential rôle in the very origin of life. The first replicating elements were presumably fragments of RNA, whose size was limited, perhaps to 100 bases or less, by the inaccuracy of their replication (EIGEN *et al.* 1981). Such small elements could only perpetuate their self-replication as parts of "hypercycles." In hypercycles, each type of RNA element programmed an enzyme, or served as a ribozyme, which catalyzed the next in a circular causal chain where, say, A enabled B to multiply, B enabled C to multiply, and C enabled A to multiply. (EIGEN *et al.* 1981).

Yet the future of a hypercycle is assured only if the hypercycle is not vulnerable to "parasitic elements", for example, a variant B' which multiplies more rapidly than B when A is present, but which does not enable C to multiply. How can hypercycles be organized or structured so that RNA variants will spread in them only if they benefit the hypercycle as a whole? For a variant B' to benefit by enhancing C's multiplication, or to suffer from hindering it, the consequences of its change must affect B' more than its competitors. This would be true if the hypercycle were replicated in many small compartments, say *protenoid* spheres or "cells" of coacervates, where a variant affects only its own compartment (EIGEN *et al.* 1981, MAYNARD SMITH 1979, 1988), SZATHMARY & DEMETER 1987). The principle here is the same one by which those parasites which make territories of their hosts are the most likely to become beneficial symbionts, and by which a farmer is most likely to care for his land if he and his descendants predictably benefit most from his improvements and suffer most from his abuses (as is true for small-holders with stable land tenure: NETTING 1989).

It is also true that if each RNA element interacts only with very near neighbors, as is true for molecules in the "reaction-diffusion" systems which generate the curious spiral waves of the Belousov-Zhabotinsky reaction, then parasitic elements will tend to disappear (BOERLIJST & HOGEWEG 1991, MAY 1991).

HONEST MEIOSIS AND THE EVOLUTION OF A COMMON INTEREST AMONG GENES

We have seen that the evolution of genuine multicellular organisms (as opposed to aggregations of cells) presupposes genetic differences between these organisms and genetic identity among any one organism's cells. Only sexual reproduction can create a population of organisms each of which is genetically unique. Sexual reproduction involves a fusion of gametes, and therefore, some form of reduction division which intervenes between the diploid zygote and the haploid gametes. Especially in organisms where one sex produces an excess of gametes, reduction division is vulnerable to genetic elements which cause their cells to attack sister cells (HAIG 1993), thereby enhancing their own representation among the organism's viable gametes.

In fact, multicellular organisms with differentiated tissues all descend from organisms which produce haploid cells by meiosis (MARGULIS & SAGAN 1986). Meiosis determines, for each autosomal locus, which of a parent's two genes at that locus a given gamete will receive. At most loci, meiosis is the fairest of lotteries. Consider, for example, a male heterozygous at two loci, **A** and **B**, on different chromosomes, whose genotype is represented as **AaBb**. Normally, a sperm has probability 1/2 of receiving **A** rather than **a**, and probability 1/2 of receiving **B** rather than **b**. Moreover, since **A** and **B** are on different chromosomes, the inheritance of **A** rather than **a**, and the inheritance of **B** rather than **b**, are independent events: the occurrence of one does not affect the probability of the other's occurrence.

What prevents alleles from biasing meiosis in their own favor? We shall find that the "fairness" or "honesty" of meiosis represents the common interest of an organism's autosomal genes (LEIGH 1971, 1977). Where there are many chromosomes, selection can enforce this common interest with almost complete success (LEIGH *et al.* 1985, LEIGH 1987). This multiplicity of chromosomes constitutes a parliament of genes where the common interest of the whole can overcome the "cabals of a few" (LEIGH 1971). The fairness of meiosis is crucial to the evolution of multicellular organisms, because it assures that an allele cannot spread unless it benefits the individuals which carry it (MAYNARD SMITH 1988; LEIGH 1987, 1991).

Let us begin by supposing that in male bearers, **A** biases meiosis in its own favor, perhaps by destroying the

a-bearing chromosome when the two pair off in the early stages of meiosis, so that 95 to 100% of the sperm produced by an **Aa** male carry **A** (destroying half a human male's sperm would not greatly impair his capacity for fatherhood), or by ensuring that its chromosome, rather than the alternative, is passed on to the egg rather than a polar body destined for destruction (ZIMMERING *et al.* 1970). Alleles which bias meiosis in their own favor are known from a very few loci in each of a wide variety of organisms (ZIMMERING *et al.* 1970, WERREN *et al.* 1988). Such a "segregation-distorter allele" **A** can spread rapidly through a population. Indeed, theory predicts that strong distortion of the meiotic segregation-ratio can enable an allele to spread a phenotypic defect through a population which causes its extinction. LYTLE (1977) experimentally confirmed this prediction by translocating the Segregation-Distorter locus from the second to the Y chromosome of *Drosophila melanogaster*, and introducing males carrying the distorter Y chromosome into cages containing normal flies. Most of the sperm received by females mating with males carrying the distorter Y chromosome carried this chromosome, so nearly all their offspring were males carrying the distorter Y. This nearly two-fold advantage of the distorter Y chromosome spread it quite rapidly through the caged populations to which it was introduced, even though many of these populations died out for lack of enough females to "carry on the race" (LYTLE 1977). In short, segregation distortion opens the possibility of a conflict of interest between a "selfish" distorter allele, and both the individual whose death it may hasten, or whose reproductive value it may impair, and the species whose extinction it may cause.

Now let us consider the effect on the **B** locus of an (unlinked) segregation distorter **A** which spreads a phenotypic defect through the population. At meiosis, **B** and **b** assort independently of **A** and **a**: no allele at the **B** locus can benefit by "riding **A**'s coattails". On the other hand, a mutant **B'** at the **B** locus which suppresses **A**'s distortion, restoring the honesty of meiosis, spares some of its bearers from the segregation distorter **A** and the phenotypic defect **A** causes. Restoring the honesty of meiosis among **B**'s descendants increases their aggregate reproductive value, so natural selection spreads **B'** through the population (LEIGH 1971, PROUT, BUNDGAARD & BRYANT 1973). Thus we may speak of a common interest of the genome as a whole in enforcing the honesty of meiosis. In effect, honest meiosis aligns the interest of each of an individual's genes with the good of that individual by allowing alleles to spread only if they benefit their carriers. What evidence is there that the common interest of the genome as a whole does enforce fair meiosis? In the first few species with chromosomally determined sex to be carefully studied, such as humans and falcons, no genetic variation in sex ratio could be

detected (WILLIAMS 1979). Significant variation in hatchling sex ratio is rare among birds (CLUTTON-BROCK 1986). Sex ratio can vary within mammal populations, but this variation appears to reflect, not distortion of meiotic segregation-ratios, but features such as weight differences between X- and Y-carrying sperm (CLUTTON-BROCK & IASON 1986). For example, variation in the female reproductive tract over the reproductive cycle, or with the animal's condition, affects sex ratio by influencing the degree of spatial segregation in X- and Y-carrying sperm (CLUTTON-BROCK & IASON 1986, pp. 386-387).

WILLIAMS (1979) used the absence of genetic variation in chromosomally determined sex ratios to question the adaptive theory of sex ratio. I believe that this absence has far broader implications. Selection on small deviations from optimal sex ratio is notoriously weak (LEIGH 1970): if such mutants were frequent, many of them would increase to substantial frequencies before selection checked their spread (KIMURA 1965, LANDE 1976A, TURELLI 1984, eq. 3.16; LEIGH *et al.* 1985). The absence of genetic variation in sex ratio suggests that mutations affecting sex ratio are extremely rare. If mutations affecting sex ratio, which can take advantage of the obvious morphological differences between the sex chromosomes, are so rare, surely mutations affecting autosomal sex-ratios are even rarer, as WU & HAMMER (1991, p. 185) argued on other grounds. Why should segregation distorters occur so rarely?

Some of LYTTLE's caged populations survived the introduction of males bearing the distorter Y, perhaps because distortion of Y against X was less extreme in these populations. A curious chromosomal non-disjunction mutant, which does not concern us further, partially restored the proportion of females produced by some of these populations (LYTTLE 1981). Other populations evolved a sex ratio slightly closer to normal during the course of LYTTLE's (1979) experiment. Loci on all chromosomes contributed to this change, suggesting that the common interest of the genome as a whole in honest meiosis is not merely a theoretical construct, but a natural phenomenon with observable effects. Over evolutionary time, segregation distorters with harmful phenotypic effects must time and again have been hung up in polymorphisms where the advantage of distorter heterozygotes just balanced the sterility or lethality of distorter homozygotes, as is true for the Segregation-Distorter locus in *Drosophila* and the *t* haplotypes of house mice today (PROUT *et al.* 1973, Lewontin and Dunn 1960, Silver 1985). Such balanced polymorphisms allow time for mutants restoring the honesty of meiosis to occur and spread. Has the restoration of honest meiosis in the face of challenges from successive harmful segregation distorters eliminated the "easy" ways to bias meiotic segregation ratios? Despite the great initial advantage

accruing to segregation distortion, distorter alleles are rather rare (WILLIAMS 1979, CROW 1991). Moreover, the means by which known segregation distorters bias meiosis in their own favor have proven extraordinarily difficult to detect (CROW 1991), as if the "obvious" means of doing so had been blocked.

VON NEUMANN & MORGENSTERN (1944) could find no theoretical basis for the idea that economic competition can work for the common good. Inconscient nature has been far cleverer: meiosis is a working model of ADAM SMITH's (1759, 1776) idea that if a society's members share, and can enforce, a common interest in rules which exclude dysfunctional modes of competition, competition among those members works for their society's good. Unlike human societies, genomes lack members rich or powerful enough to bend the rules in their own favor. Arranging genes in chromosomes, however, seems to have been a necessary precondition of honest meiosis: transposable elements, which can jump from one chromosome to another, can spread without benefitting their carriers (CHARLESWORTH & LANGLEY 1991).

The evolution of eukaryotes required the *subordination* of lineages of quondam parasites or aliens to the good of their host cells. Sexual reproduction among organelles is rather rare, (THOMPSON 1994). Mitochondrial genomes of yeast and plants do recombine repeatedly, but chloroplast genes recombine only within an individual plastid, and genes in animal mitochondria may never recombine (BIRKY 1991, p. 117). Most eukaryotes, by contrast, engage in sexual reproduction rather frequently. Apparently, in animals organelles no longer contribute to the adaptive evolution of their hosts. The evolution of complex multicellular organisms involves mechanisms meant to ensure that an individual's cells serve that individual (BUSS 1987). It would be just to remark that an individual's cells had better hang together, lest they hang separately: cells do share a common interest in their individual's welfare. Yet, among such animals as insects and chordates, the sequestration of the germ line represents a genuine *subordination* of cells to individuals. The honesty of meiosis is a very different story: it represents a common interest among equals, a sort of reciprocal altruism.

ANIMAL SOCIETIES

Group living appears when it is easier for an animal to avoid being eaten, or to acquire information about, or access to, food or other resources by living in a group. Once animals aggregate in groups, however, there seems to be a dichotomy between groups in whose evolution subordination of some individuals to others plays a prominent rôle, and groups which evolve by a more nearly symmetrical reciprocal altruism.

Social Insects

Subordination has played an essential rôle in the evolution of social behavior among hymenoptera and termites. The varied degrees of social behavior allows one to divine the stages by which social behavior evolved (WEST-EBERHARD 1981). Among insects which live in groups, an insect's reproductive success hinges primarily on its ability to win in social competition, rather than its capacity for coping with other aspects of its environment (WEST-EBERHARD 1979). Among insects which cannot reproduce successfully outside a group, some resources needed for reproduction will be in short supply within a group, and competition for these resources may create "winners" and "losers." This circumstance often favors a division of labor where losers help related winners reproduce, by performing tasks for which the winners are less suited, or lack time for (WEST-EBERHARD 1981). For example, females which are aggressively defending nest cells and newly laid eggs have little time to forage. On the other hand, losers whose newly laid eggs have just been destroyed to make room for a dominant's egg may still retain the instinct, appropriate to a wasp whose ovary now lacks a mature egg, to care for their dominant's neglected brood. Moreover, the ovaries of wasps which dominants prevent from laying eggs often degenerate, and the continued lack of a mature egg in the ovary may prolong the loser's tendency to care for the winner's brood (WEST-EBERHARD 1987). Thus group living can transform a tendency for social parasitism among winners and an instinct to care for brood among eggless losers into the basis for a division of labor essential to the group's welfare.

Even after division of labor is established, there is abundant opportunity for conflict. For example, unmated hymenopteran workers can lay male eggs. As an ant queen is more closely related to her sons than her grandsons, it pays her to prevent workers from laying eggs. In many ant species, queens tend to attack those workers with the most developed ovaries (HEINZE *et al.* 1994). Ant workers are also more closely related to their sons than their nephews, so a worker benefits from laying eggs while making her colleagues help the colony. Thus conflict also arises over which workers, if any, may reproduce (HEINZE *et al.* 1994). Similar conflicts also arise within colonies of primitive termites (ROISIN 1994). Here, young termites stay in their nest and help their parents before growing wings and flying off to found new colonies. Helping their parents enhances their colony's survival, which assures the young termite's own life support system. Nevertheless, a termite worker would benefit by growing wings as fast as possible and flying off to reproduce, while having its siblings continue to help its parents. Accordingly, workers fight, biting each other's wing-buds, over which of their number should graduate to the reproductive stage (ROISIN

1994). As in human societies, it pays to reap the profit while others do the work ... if one can get away with it.

The conflicts of interest between winners and losers, or between different losers, can be eliminated by (nearly) annihilating a loser's chance of personal reproduction, that is to say, by differentiating reproductive queens and non-reproductive workers into permanent castes (ROISIN 1994). If a colony's workers cannot reproduce on their own, they share a common interest in their queen's reproductive success. A honeybee queen nearly eliminates worker reproduction by mating with 18 to 20 males and mixing the sperm thoroughly. A worker benefits by eating eggs laid by half-sisters, because a half-sister's son is less closely related to her than a brother, a son of her queen (RATNIEKS & VISSCHER 1989). Because the sperm are well mixed, most of a worker's comrades are half-sisters, which eat any of her eggs that they find. Accordingly, most of the eggs that workers do lay, are eaten. Perhaps as a result, workers in colonies with healthy queens lay few eggs (RATNIEKS 1993). By eating each other's eggs, workers develop a common interest in enhancing their queen's reproduction. The queen need do nothing further to force them to help (RATNIEKS & VISSCHER 1989). A leafcutter ant queen also mates with several males (HÖLDOBLER & WILSON 1990, p. 600), but an army ant queen mates only once (FRANKS & HÖLDOBLER 1987). Ant workers, however, rarely lay eggs in colonies with healthy queens, because these queens produce a pheromone which "prevents" them from doing so. Why should this pheromone be obeyed? Apparently, in complex ant societies, ant workers lay eggs so much more slowly than their queen that they do better to help her (HEINZE *et al.* 1994). Moreover, the larger and more complex an ant colony, the more its workers tend to treat their queen as a valued resource rather than as a rival (HÖLDOBLER & WILSON 1990, p. 194). Like queen honeybees, queens of complex ant societies need not *force* their workers to do suitable labor: intragroup conflict is a characteristic of smaller, less complex, ant societies (HEINZE *et al.* 1994).

Although an ant queen creates a common interest with her workers essentially by sterilizing them, ant workers are not merely extensions of their queen's body. When the queen's interest does conflict with the common interest of her workers, the common interest of the workers prevails. In monogynous ant colonies, workers benefit most by devoting three times as much effort to raising female as male reproductives, while it is in the queen's interest to devote equal effort to each: the sex ratio favored by the workers (which happens to be the one better for the *species*) is the one the ant colony adopts (TRIVERS & HARE 1976, CHARNOV 1982). The power of ant workers is illustrated in other ways. When an army ant (*Eciton burchelli*) colony divides, workers of the "new" half choose their queen and her mate (FRANKS & HÖLDOBLER 1987).

Honeybee colonies are marvels of self-organization (SEELEY & LEVIEN 1987, SEELEY 1989a). A honeybee colony adjusts its foraging to the changing pattern of available pollen and nectar through the independent reactions of each forager to the quality of its own food source, the time required for food storer bees to accept their nectar, and, perhaps, the protein content of the gland secretion which returning foragers receive from nurse bees (SEELEY *et al.* 1991, SEELEY 1989b, 1994; CAMAZINE 1992). More generally, honeybee workers adjust their division of labor to changes in the colony's needs. Honeybee workers pass through a sequence of tasks as they age, beginning with the least risky ones, such as nursing the brood, which are performed within the nest, and ending as foragers, the riskiest task of all (ROBINSON 1992). It is as if workers were trying to protect their future prospects of reproduction as much as possible, for as long as possible (WEST EBERHARD 1981). Ironically, this expression of worker self-interest simplifies the division of labor. A honeybee worker's progress from one task to another is governed by its titer of juvenile hormone (ROBINSON *et al.* 1989). Workers with different fathers are differently represented at the colony's tasks (ROBINSON *et al.* 1989), perhaps because a worker's genotype influences her sensitivity to different environmental cues for choice of task (ROBINSON & PAGE 1988). A worker's "*cursus honorum*", however, adjusts in response to her colony's needs. If most of the colony's older workers are removed, some of the remaining workers become foragers at an earlier age than usual. If most of the colony's younger workers are removed, some of the remaining younger workers continue caring for the brood longer than usual (ROBINSON *et al.* 1989): indeed, if all brood nurses are removed, some foragers will revert to nursing brood (ROBINSON 1992). These shifts apparently reflect adjustments in titer of juvenile hormone to the changed conditions of the colony (HUANG & ROBINSON 1992).

Ants also provide striking examples of "self-organized" societies. For example, a colony of army ants, *Eciton burchelli* contains perhaps a half-million workers. By following a few simple rules, the ant's foragers collectively form become an effective team for obtaining prey and transporting it back to the bivouac. These ants form a bivouac of their own bodies which regulates temperature inside it to $\pm 1^\circ \text{C}$. Despite the simple behavior and the apparently limited attainments of the individual workers, army ant colonies are remarkably adaptable and efficient foragers (FRANKS 1989). Leafcutter ant colonies, with their millions of workers, exhibit a remarkably subtle and refined division of labor (HÖLDOBLER & WILSON 1990).

Nonetheless, there is room for conflict in complex societies of both bees and ants. Because a honeybee queen mates with many males, workers rearing larvae destined to

be queens would benefit by discriminating in favor of full sisters (PAGE *et al.* 1989), a form of nepotism ants avoid by mating only once. Interestingly, honeybee workers caring for future queens discriminate weakly, if at all, in favor of full sisters (RATNIEKS & REEVE 1992). On the other hand, a honeybee queen and her workers favor similar sex ratios among their colony's reproductives (RATNIEKS & REEVE 1992), while, as we have mentioned, in an ant colony born of a single queen, once mated, the queen and her workers favor quite different sex ratios among the reproductives (TRIVERS & HARE 1976).

Vertebrates

Many kinds of birds and mammals also live, or at least forage, in groups. Again, they do so either because group living provides better protection against predators, or because groups defend resources more successfully against competitors, or because foraging as a group is more efficient. Most of these groups exchange migrants far too often for selection among groups to override within-group selection. Some social groups are not even breeding units, so there is *no* selection among groups to favor cooperation.

A striking example of social groups which are not breeding units is "mixed species bird flocks," in which several species of birds forage together. Mixed species bird flocks are a characteristic feature of the wet tropics (MOYNIHAN 1962). In many such flocks, a species is seldom represented by more than one mated pair, perhaps with attendant young (MOYNIHAN 1979, p. 92; GRADWOHL & GREENBERG 1980; MUNN 1985). A flock's membership may vary throughout the day, yet, day after day, the same birds, of the same species, join the flock (MOYNIHAN 1962, p. 8; GRADWOHL & GREENBERG 1980; MUNN 1985). In some kinds of flocks, individuals of a few core species are nearly always present: these birds jointly traverse a fixed circuit or territory over the course of the day. Other birds with smaller territories join the flock when it crosses their territories, while some birds with territories large enough to include several flocks move from one flock to another (GRADWOHL & GREENBERG 1980). When neighboring flocks meet, some members may defend their flock's territory by singing at, or displaying against, conspecifics in the other flock (GRADWOHL & GREENBERG 1980, MUNN 1985). Indeed, a flock's circuit is often the jointly defended territory of single pairs of each of two or more core species of that flock.

Why do these birds flock together? Insectivorous birds can eat insects which their neighbors have flushed (MOYNIHAN 1979, p. 92), and often can no longer reach, just as ant-following antbirds eat insects flushed by an advancing swarm of army ants (WILLIS 1967). Nonetheless, in a mixed flock, each species searches for somewhat different food, or searches for its food in somewhat different

places or somewhat different ways (JONES 1977), as if to reduce competition. Although frugivorous birds can sometimes find food by watching each other (MOYNIHAN 1979, p. 92), the main benefit they derive from the group is probably protection from predators. There are many more eyes to watch for predators, so a bird can spend more time feeding and still expect to receive earlier warning of a predator than when feeding alone (MOYNIHAN 1979, p. 92). Birds in a flock can often drive smaller predators away by "mobbing" them. Just as it is harder for a predator to "home in" on a fish when it is in a school, it may be harder for a predator to home in on a bird which is part of a flock (MOYNIHAN 1962, pp. 119-120). Indeed, a bird may sacrifice very little for the benefits it obtains by joining a flock. Even alarm signals may benefit the signaller. Not only may the signal prompt the group to engage in co-ordinated mobbing or confusing escape, but the signal may also inform the predator that, since it has been noticed, its chances of success with *this* group are at an end (SMYTHE 1977). The community of interest among a bird flock's members has had an impact: the social organization of these flocks is sometimes rather complex (MOYNIHAN 1962), and there has been some coevolution among the species of a flock to facilitate flocking behavior (MOYNIHAN 1968). Yet it is hard to imagine how some group members could "force" others to cooperate. Are mixed bird flocks examples of mutualism without enforcement?

Coati females form much more tightly knit social groups. Female coatis and their young can only prevent the larger males chasing them away from fruiting trees by banding together (GOMPPER 1994). Daughters usually stay with their natal group all their lives, while males leave the group when mature, and live alone (KAUFMANN 1962, RUSSELL 1982). There are many other advantages to living in a band. Females defend, and often nurse, each other's young (RUSSELL 1982, GOMPPER 1994), and there are more eyes to watch for predators, which allows each individual to spend more time foraging (RUSSELL 1982). They groom each other for ectoparasites (KAUFMANN 1962). Coatis also help each other find fruit: mutual care of the young allows adult females to wander off in search of fruiting trees. Older females apparently remember the location of, and lead their bands to, distant fruiting trees at appropriate times (RUSSELL 1982).

In coatis, males leave their natal bands before they become sexually mature, while females normally stay in their natal bands all their lives (KAUFMANN 1962). In most coati bands, therefore, adult females are closely related (KAUFMANN 1962, GOMPPER 1994). Kin selection obviously enhances cooperation among band members. Nonetheless, if a band dwindles sufficiently, it will try to join another (KAUFMANN 1962). Even though the newcomers are treated as "second-class citizens" who are groomed less and suffer more aggression, joining another band is important. Coatis

in larger bands are less likely to be displaced from fruiting trees by lone male coatis, potentially predatory tayras, or other animals, and there are more animals to share the watch for predators (GOMPPER 1994). Other kinds of animals also stay in groups out of an evident fear of being alone. In groups with leaders, other members follow when the leader moves on, whether or not they have finished resting or eating, as if the danger of being alone outweighs any advantage of staying. Even rams, which compete fiercely during the mating season, associate in groups at other times of year.

Social organization is yet tighter in many monkey groups. Monkeys also join in groups to help each other fend off competitors, share the watch for predators, and help each other protect the young. In this process, they also share the task of teaching the young how to find food and fit into their society (ROWELL 1975, JOLLY 1985). Here too, the presence of a female past reproductive age who remembers where to find food or water in a time of unusual scarcity can be a matter of life or death for the whole troop, which amply repays patience with the various disabilities associated with her age (ROWELL 1975).

In some monkey species, group members appear to join in encouraging or forcing a recalcitrant fellow member to behave more in accord with the good of their group (ROWELL 1975). The extent, appropriateness and effectiveness of such enforcement of a monkey group's common interest warrants closer study.

In many species, a monkey group includes several adult females, their offspring, and a single adult male. In some of these species, the resident male lacks the power to keep other males from mating with "his" females, nor can he force his females to cooperate for the good of his group (CHISM & ROWELL 1986, ROWELL 1987). Is the common interest among the monkeys of such a group strong enough to favor cooperation even when there are no mechanisms to enforce it?

Are there other groups whose individuals share a strong enough common interest for individuals to cooperate without threat of enforcement? What could be the basis of this common interest? In those many species of vertebrates where individuals aggregate to get help from others in avoiding predators, an individual's chance of being eaten may depend on how well it co-ordinates its activities with those of the rest of the group. Predators may return to groups where they have previously succeeded in making a kill, much as burglars return to houses which they have already successfully entered. If, as seems quite probable, predators focus on groups which previous experience has shown to be more easily attacked, perhaps because their defenses were less well coordinated, an individual's advantage could coincide quite closely in certain respects with the good of its group, irrespective of any "group selection".

SMITH (1986, p. 73) aptly summarized the situation with respect to vertebrate social groups:

... social behavior of any appreciable complexity and persistence makes the participating individuals interdependent. To get the various advantages that accrue to being social each participant must in some ways and to some extent accommodate the others. For instance, in many species an animal cannot survive or breed without belonging continuously to a group. Even a dominant member of such a group must actively tolerate and even encourage the presence of the others, for without them it is alone. Subordinate individuals accommodate to a much greater extent than do dominants, but *all* accommodate. This accommodation is a widespread sort of cooperation: individuals acting for mutual benefit because each needs a continuing relationship with the others. Accommodation between individuals is essential for the formation and subsequent maintenance of organized groups.

THE VARIOUS DEGREES OF MUTUALISM AND THEIR CAUSES

Mutualisms can be classified in many ways. In some, coevolution is so strict that the lines of descent of the two partners are inextricably linked, as is true for organelles and their host cells and (in a different sense) for an army ant colony's workers and their queen. In others, such as the various members of a mixed-species bird flock, coevolution is very "loose": such flocks are not "units of selection" in the sense of Lewontin (1970). Some mutualisms are "unequal" ... one member of the mutualism is decidedly subordinated to the other, as organelles are to their host cells, or an army ant colony's workers to their queen; others, such as those among the genes of a genome or the birds of a mixed flock, are relatively "egalitarian." If one partner of a mutualism is an endosymbiont or "inhabitant" (Law and Lewis 1983) of the other, the endosymbiont may be more susceptible to retaliation for failures to cooperate. Some mutualisms, like those among genes of genomes or between organelles and their host cells, are tight, even obligate, with an extraordinary degree of interdependence and co-ordination among the partners; others are looser and more facultative, such as that linking the birds of a mixed flock, or a tree species and any one of the many animals which might disperse its seeds. Why this great diversity of expression among mutualisms? To answer, we will

consider the variety of ways by which a common interest among partners of a mutualism may be enforced.

STRICT VERSUS LOOSE COEVOLUTION AND SELECTION AMONG GROUPS

Remarkable harmony and interdependence can evolve among the partners of a mutualism by means other than strict coevolution. Yet coevolution between the partners of a mutualism which is so strict that one partner, or its genes, are passed on only to the young of its current "host", enforces harmony, and often leads to utter interdependence among the partners. Such coevolution redefines the units of evolution, replacing selection among members within groups by selection among these groups (MAYNARD SMITH 1988).

What conditions allow the development of strict coevolution, where propagation of one mutualist's genes depends on the successful reproduction of the other, as in symbionts which can only be transmitted "vertically"? How effective is strict coevolution in shaping a mutualism? What are the costs and benefits of strict coevolution to the dominant partner?

Strict coevolution normally arises when either

1. parasites make territories of their hosts, thereby setting the stage for their parasites' subjection to an overwhelmingly effective selection among populations inhabiting different host individuals, as happened to the ancestors of intracellular organelles, or
2. one partner in a mutualism manipulates the others in a manner that subjects them to an effective selection among groups in the dominant partner's interest, as happened in the evolution of multicellular organisms and advanced social insects.

How effective is strict coevolution in shaping mutualisms? Strict coevolution is a reliable means of transforming parasites into mutualists. This is shown, for example, by the nematodes parasitizing the wasps which pollinate a given species of fig tree. The nematodes infect newly hatched female wasps in their natal fig fruit, and are carried by the outgoing female wasps to the fruits they pollinate. After the wasp lays its eggs in the "fruit" (actually, a head of flowers turned outside in, so the flowers are enclosed in a "fruit wall": CORNER 1940) it pollinates, its nematodes consume it and reproduce, and the young infect the next generation of newly hatched females, repeating the process. In those species of fig tree where each fruit is pollinated by a single female wasp ("single-foundress figs"), a nematode can only reproduce by infecting the offspring of its host. Here, the coevolution of wasp and nematode is as strict as can be, and the nematode

does not diminish the reproductive success of its host. In those species of fig tree, many of whose fruits are pollinated by two or more wasps apiece, a nematode's fate is less closely linked to the health of its host. Indeed, the higher the average number of pollinating wasps per fig fruit, the more the nematodes reduce the reproductive success of the wasps they infect (HERRE 1993). As the conflict of interest between the wasps and the nematodes they carry appears pretty fundamental, only strict coevolution can "tame" the nematodes. The number of pollinating wasps per fig fruit, however, is governed primarily by factors other than parasitic nematodes (PATIÑO *et al.* 1994), and there seems to be no tendency for nematode "virulence" to decline over evolutionary time.

How does strict coevolution affect a mutualism? Leafcutter ants and their allies of the tribe Attini cut leaves, or gather vegetable matter or insect frass or corpses, on which they plant a symbiotic fungus which digests otherwise indigestible parts of their food (HÖLLDOBLER & WILSON 1990). Different groups of leafcutter ants vary greatly in how strictly they coevolve with their fungi (CHAPELA *et al.* 1994, HINKLE *et al.* 1994). Advanced leafcutter ants take their leaves into a vast underground nest where they maintain a fungus farm on leaf fragments. In these species, a queen ant flies off with a mouthful of fungus from the parental nest to establish a new colony (HINKLE *et al.* 1994). Her workers nibble the parts of the fungus that would otherwise develop into reproductive structures, pluck out alien fungal growths, and spread antibiotic secretions about the nest which prevent fungal spores from germinating (HÖLLDOBLER & WILSON 1990, p. 599). The ants thereby prevent exchange of fungi between leafcutter ant colonies, and render the fungus's reproduction entirely dependent on that of its host colony. Advanced leafcutter ants have thereby subordinated the evolution of their fungus to serve the good of leafcutter ant colonies (LEIGH 1991). Indeed, this subordination has rendered the fungus nearly (but not quite absolutely) asexual (HÖLLDOBLER & WILSON 1990, CHAPELA *et al.* 1994, HINKLE *et al.* 1994). Subordinating fungus- to ant-evolution causes the ants and their fungus to "co-speciate", or speciate in parallel, so that their phylogenies coincide. This subordination may have been crucial to the efflorescence of abundant species of advanced leaf-cutter ants with extraordinarily complex societies: not just any fungus will digest freshly cut leaf fragments of so many kinds of plants (HINKLE *et al.* 1994), whereas the range of fungi which will grow on insect frass or dead vegetation may be much wider. Primitive attine queens, however, have not been seen to bring their fungus from the parental nest. Perhaps because these ant queens lack this habit, phylogenies of primitive leafcutter ants and their symbiotic fungi are quite discordant: close relationship among primitive attines does not necessarily imply close

relationship among their fungi, and vice versa (CHAPELA *et al.* 1994). Do primitive attines derive some advantage from not domesticating their fungus so thoroughly?

An answer is suggested by reefbuilding corals and their zooxanthellae: the freedom to choose one's symbionts is sometimes valuable. Thanks to their symbiotic zooxanthellae, corals are the marine equivalent of carnivorous plants. Their zooxanthellae enable corals to obtain energy from sunlight, while corals obtain nutrients and vitamins for themselves, but apparently not for their zooxanthellae, by trapping small marine animals (TRENCH 1987, p. 557; MUSCATINE *et al.* 1989). On the whole, the phylogenies of coelenterates and their zooxanthellae do not match: closely related hosts may harbor very divergent zooxanthellae and vice versa (ROWAN & POWERS 1991). Although some coral species pass zooxanthellae from mother to young through the egg, other corals must "call" their symbionts from the surrounding water (TRENCH 1987), as a flowering plant calls its pollinators from the surrounding forest. Two coral species, *Montastrea annularis* and *Montastrea faveolata*, which acquire their symbionts from the surrounding water, each shelter three genetically divergent strains of zooxanthellae, and an individual colony of these species sometimes possesses two strains (ROWAN & KNOWLTON 1995). These *Montastrea* cannot subordinate the evolution of zooxanthellae to that of their hosts. On the other hand, different strains of zooxanthellae may function best at different depths. Moreover, it may sometimes pay a coral to expel its zooxanthellae, in the hope that it may be reoccupied by a strain more suitable to current conditions (ROWAN & KNOWLTON 1995). Sometimes, strict coevolution with symbionts can unduly restrict the host's options.

MUTUALISMS WITHOUT BONDAGE

As we have seen, strict coevolution is not the only, or even the most usual, means by which mutualisms evolve. Sometimes, as in certain corals, strict coevolution is disadvantageous to both partners of a mutualism. Sometimes, as in leafcutter ants, mutualism precedes the advent of strict coevolution. How do mutualisms evolve in the absence of strict coevolution?

When Individual and Group Advantage Both Matter

The good of the group is sometimes a relevant factor, but not the only one, in evolutionary change. This is the case for selection on the sex ratio among the offspring of wasps which pollinate fig trees (FRANK 1985, 1986; HERRE 1985, 1987).

As we mentioned a few paragraphs ago, each species of fig tree has its own species of pollinating wasp (CORNER 1940). Consider a fig species where a fixed number N of fertilized, pollen-bearing foundress wasps

enter the syconium, pollinate its flowers, and lay eggs in some of them: their young mate among themselves and the fertilized females fly off in search of new figs to pollinate (CORNER 1940, JANZEN 1979). The N mated females pollinating a fruit may be considered a "mating trait-group": their fruit serves as a "retort" in which they elaborate a new set of mated females. Schematically, we assume that these newly mated females join a common pool from which the next generation's mating trait-groups are drawn at random.

Here, two levels of selection affect the sex ratio (the ratio of males to females) among the offspring of a fruit's N foundresses (COLWELL 1981). Selection within each fruit to increase the proportion of an individual's genes carried off by the fertilized females favors producing as many male as female young (FISHER 1930). Selection among different fruits to increase the number of fertilized females each fruit contributes to the pool from which the next generation's mating trait-groups are formed, favors producing as many females as possible, and only enough males to fertilize these females.

The effectiveness of selection is the product of its intensity, and the genetic variance of the characteristic under selection (FISHER 1930). Let the heritable (additive) genetic variance be V . Since each fruit is pollinated by N wasps, the average genetic variance within mating trait-groups is $(N - 1)V/N$, and variance among trait-groups is V/N . Theory predicts, and observation confirms (Appendix, section 5, HERRE 1985), that the smaller N , the more powerful selection among, relative to that within, trait-groups. Thus the smaller N , the more female-biased are offspring sex ratios. In the limiting case where $N = 1$ (each fruit is pollinated by a single wasp), there is no opportunity for selection within trait-groups, and only enough males are born to fertilize the females (HERRE 1985).

Another example where group advantage exerts some influence is provided by "matrifocal" societies such as bands of female coatis (GOMPPER 1994) or troops of ringtail lemurs (JOLLY 1985). Daughters of a coati band remain in it all their lives, while males emigrate before reproducing. Let each female conceive each young by a different male, selected from an infinite pool. Let the band have a fixed number N_f of adult females. Let $G(t)$ be the average coefficient of consanguinity (CROW & KIMURA 1970, p. 68) between different females in the band, the probability that two homologous genes sampled at random from different females in the band are recently descended from the same gene. Then we may calculate $G(t + dt)$ as the probability that both females alive at time t are still alive at time $t + dt$, $(1 - mdt)^2 \approx 1 - 2mdt$, times $G(t)$, plus the probability that one of them dies during this interval, $2mdt$, times the expected consanguinity between the survivor and the dead female's replacement. This last we figure by saying that the probability is $1/N_f$ that the

replacement's mother is the survivor, in which case $G = 1/4$, while the probability is $(N_f - 1)/N_f$ that the replacement's daughter is not the survivor, in which case the expected consanguinity is $G(t)/2$. The factor $1/2$ enters because the replacement is the daughter of a band member and an unrelated male. At equilibrium,

$$G(t + dt) = G(t) = G(t)(1 - 2mdt) + 2mdt \left[\frac{1}{4N_f} + \left(\frac{N_f - 1}{N_f} \right) \frac{G(t)}{2} \right] \quad (1)$$

Here, G 's equilibrium value is $1/[2(N_f + 1)]$. Since an outbred individual's consanguinity with herself is $1/2$, a coati should make a sacrifice for a fellow band member if the resulting prospective loss in its reproduction is less than $2G$ times its beneficiary's gain. Bands average about 4 adult females apiece (RUSSELL 1982), so band members tend to be rather closely related (KAUFMANN 1962). If coatis often face alternative solutions to a problem which differ far more in their effects upon neighbors than in benefit to themselves, the substantial relationship between ~~between~~ adult females in a band must enhance its cohesion considerably.

2. Reciprocal Altruism: Mutually Enforced Common Interest

The problems involved in the evolution of many mutualisms are caricatured by the "iterated Prisoner's Dilemma" (AXELROD 1984). The "Prisoner's Dilemma" is a 2-person game where each player can Cooperate or Defect. If both cooperate, each earns 3 points. If one cooperates and the other defects, the defector earns 5 points and the cooperator, 0. If both defect, each earns 1 point. Defection gives the greater profit, whatever the opponent's play. On the other hand, if the same pair of individuals play each other repeatedly, the average profit for each is higher if they both cooperate than if they both defect. Thus the players share a common interest in cooperating which, however, can be vitiated if one player succumbs to the temptation of the higher short-term profit obtainable by defecting on a cooperating partner.

How can players manage to enforce their common interest in cooperation? Invariable cooperators are vulnerable to defectors: the only way to cope with invariable defectors is to defect. To examine this problem, let us imagine a tournament, where the same pair of players play each other repeatedly, but where, after each game, a player has a small probability δ of switching partners. Let each player play by a strategy or rule, and choose a strategy anew after every m plays. The probability w_i that a player chooses strategy i is the proportion w_i of the total earnings of the tournament's last m plays accruing to players using strategy i . If the tournament begins with a preponderance of invariable defectors, cooperation can only take root if players tend to

have partners which use the same strategy (AXELROD & HAMILTON 1981). If players do "cluster" in this fashion, then "Tit for Tat" ... in game 1 cooperate, in game $n + 1$, play the opponent's play of game n , is a good way for cooperation to spread through a world of defectors (AXELROD 1984, NOWAK & SIGMUND 1992). Once "Tit for Tat" prevails, "Win-stay, Lose-shift" ... if, in game n , a play earns ≥ 3 points, use it in game $n + 1$, otherwise shift ... becomes advantageous, especially in an error-prone world where the opponent's play is sometimes misread. "Win-stay, Lose-shift" cannot be displaced by invariable cooperators, whose spread would pave the way for invariable defectors. "Win-stay, Lose-shift" is also derailed less seriously than "Tit for Tat" when a cooperation is mistakenly read as a defection (NOWAK & SIGMUND 1993). "Tit for Tat" and "Win-stay, Lose-shift" are theoretical embodiments of a sometimes cynical reciprocal altruism. The prospect of repeated interaction, with the opportunity this repetition offers for retaliation, is essential for enforcing the common interest in cooperation.

Hamlets, *Hypoplectrus nigricans*, simultaneously hermaphroditic coral reef fish, use "Tit for Tat" to enforce cooperation in reducing the "cost of sex" (FISCHER 1980, 1981, 1988). The "cost of sex" arises because a sperm is far smaller than the egg it fertilizes, yet a successful sperm contributes as many genes to future generations as a successful egg (MAYNARD SMITH 1978). Thus a hermaphrodite should devote as much effort to male as female functions (MAYNARD SMITH 1978, pp. 39-40). Males which provide no parental care devote their effort to competing for fertilizations. They may fight rival males, display to attract females, or produce excess sperm. Hamlets avoid competition for fertilizations by pairing off and trading eggs for each other to fertilize (FISCHER 1980). Thus, when functioning as a male, a fish need expend only the effort, and the sperm, required to fertilize its partner's eggs. Egg-trading hamlets have testes which are small relative to their ovaries (FISCHER 1981), relatively far smaller than related, less cooperative seabasses such as *Serranus tortugarum* (FISCHER 1987). Hamlets have thus greatly reduced the cost of sex. How do they discourage cheaters which fertilize eggs without offering eggs in return for its partner to fertilize? Hamlet pairs spawn in a series of bouts, alternating sex rôles after each bout (FISCHER 1980). In the first bout, one partner acts as female, offering eggs which the other fertilizes. In the second bout, they exchange sex rôles, the quondam male now offering eggs in return for those its partner supplied in the preceding bout, and so forth. More eggs tend to be offered in later bouts, as if confidence were building up. If, however, one partner tries to cheat by playing the cheaper male rôle twice or thrice in a row, cooperation is at an end, and the cheater must find, and take the time to inspire confidence in, another mate. Why this mode of

avoiding the cost of sex is so rare, is something of a mystery (FISCHER 1988).

Cooperation can also be enforced by retaliation against cheaters on an evolutionary time scale. Thus the honesty of meiosis is maintained, as we have seen, by selection for mutants which suppress the effects on meiotic segregation-ratios of segregation distorters. Evolutionary retaliation appears to have maintained the honesty of meiosis by successively eliminating the various means by which alleles might bias meiosis in their own favor (CROW 1979). Given the slowness of evolutionary retaliation, the ability to eliminate the means by which cheating can occur may be the feature which makes it effective.

3. Mutualisms whose Partners do not Enforce Reciprocity

Some mutualisms need not be enforced by punishing cheating partners. It pays cliff swallows, *Hirundo pyrrhonota*, to reveal the presence of an insect swarm to conspecifics because the swarm is less likely to "shake loose" from the swallows, the more swallows are present. Similarly, evening bats, *Nycticeius humeralis*, which nest in colonies of a few hundred, nurse the young of other mothers, perhaps because this will eventually increase the number of bats looking for insect swarms (CONNOR 1995).

A particularly elaborate example of "unenforced mutualism" is provided by male long-tailed manakins, *Chiroxiphia linearis*, at Monteverde, Costa Rica. Male manakins aggregate in teams of ten or more to attract females. One member of each team, its alpha male, garners all his team's matings, but he depends on his team's beta male for close cooperation in the energetic dancing and duet calling required to attract females (MCDONALD & POTTS 1994). The team's beta male is not normally related to its alpha, nor is the beta provided any immediate incentive for cooperating. Why does the beta tolerate a laborious servitude, which can last five years or more?

The answer is that *i.* females only mate with alpha males which are the heads of teams, and *ii.* when the alpha male dies, his beta inherits both the alpha's position and his female "clientèle" (MCDONALD & POTTS 1994). A female visits several teams, but during a given reproductive season, she usually mates with only one team's alpha male. If her team's alpha male dies and his beta replaces him, she remains faithful to that team unless the vigor or quality of her team's display decays markedly (MCDONALD & POTTS 1994). Females prefer the teams with the most vigorous and best coordinated dancing and singing, that is to say, teams whose members cooperate most effectively. Female choice thus enforces behavior as orderly as that ascribed to the celebrated queues at British bus stops, where newcomers invariably go to the end of the line and do not try to push or sneak ahead of their predecessors.

Just as choosy females enforce cooperation among lekking manakins, predators or competing groups enforce

cooperation in many other social groups. In all these cases, failure to cooperate effectively hurts the individual as well as his group. Failure to blend in with other members of a school of indistinguishable fish may help a predator home in upon, and eat, the deviant. An ill-coordinated group may attract repeated visits from the same predator, which may leave the group too small to defend resources against competing groups.

Spatial patterns of interaction and competition can markedly influence the level of cooperation (Appendix, §§ 4-5). If two contestants play Prisoner's Dilemma repeatedly, invariable cooperators always lose to invariable defectors, and cooperation can only be enforced by strategies which punish defectors. On the other hand, there are spatial variants of Prisoner's Dilemma where inveterate cooperators coexist indefinitely with inveterate defectors even though there are no means of *enforcing* a common interest (NOWAK & MAY 1992). Imagine a tournament with players arranged in a square $n \times n$ array. In each round, every contestant plays Prisoner's Dilemma with himself and each of his eight neighbors. When two cooperators play, each wins three points; when a cooperator plays a defector, the defector wins $3b$ points ($b > 1$) and the cooperator 0; and when two defectors play, each wins 0. After the round is finished, an individual is replaced by the one of his nine neighbors (including himself) who won the most in his nine games of that round. For $b \leq 1.8$, the tournament stabilizes with over half its players as cooperators (NOWAK & MAY 1992, 1993). Allowing defectors to win points apiece, $\epsilon \ll 3$, when they play each other, which ensures that defection is superior to cooperation in any individual play, has little effect on the tournament's outcome (NOWAK *et al.* 1994a, b). The more scope for error in assessing who wins, however, the higher the proportion of defectors when the tournament stabilizes (NOWAK *et al.* 1994a, b). Making each individual play the game with a much larger array of neighbors also favors defectors (NOWAK *et al.* 1994a, b).

4. Mutualisms from Mixed Motives

Mutualism can arise from any combination of kin selection, natural community of interest, and enforcement.

Kin selection and enforcement.— The success of a bee-eater's nest is increased markedly by the presence of helpers (EMLEN & WREGE 1992). Bee-eaters often interrupt nesting attempts of their sons, to force them to help at the parental nest. The sons thus harassed often accept the rôle thus forced upon them. Sons are as closely related to their full siblings as to their offspring, so, if their help sufficiently enhances the productivity of the parental nest, they lose nothing by staying to help. On the other hand, parents are more closely related to their children than their

grandchildren, so it pays the parents to retain their offspring as helpers at the nest (EMLEN & WREGE 1992).

b. Community of Interest and Enforcement

i. One-sided Enforcement.— In some mutualisms, one partner may cooperate because its own future depends on doing so, while it retains the power to enforce cooperation from the other partner.

The mutualism between yuccas, *Yucca* spp. and their pollinating moths, *Tegeticula* spp. (Prodoxidae) illustrate this circumstance and provide clues to its origin. *Tegeticula* moths lay eggs in yucca flowers, and must pollinate these flowers if their larvae are to have seeds to eat. Indeed, *Tegeticula* have evolved special structures with which they actively pollinate yucca flowers (PELLMYR & THOMPSON 1992). In theory, a yucca moth could increase its reproductive output by converting *all* its host's seeds into young yucca moths, to the detriment of its host's reproduction (and the eventual hurt of yucca moths themselves). Yuccas, however, restrict the proportion of seeds their moths eat by aborting flowers which contain too many moth eggs (PELLMYR & HUTH 1994).

A related moth, *Greya politella* (Prodoxidae) incidentally pollinates flowers of the saxifrage *Lithophragma parvifolium* in the course of laying eggs in flower heads of this species, on which this moth is a specialized seed predator. This saxifrage has other pollinators, so pollinating its flowers is not crucial to the survival of the egg-layer's larvae (PELLMYR & THOMPSON 1992). If, however, this saxifrage were to exclude other pollinators, this moth would have to pollinate its flowers to make food for its larvae. As *Greya politella* (like most seed predators: JANZEN 1980) preys on the seeds of only one species of plant, excluding other pollinators would favor this seed predator's transformation into a faithful, species-specific pollinator. At this point, the host plant can ensure mutualism by evolving the ability to restrict the proportion of seeds eaten by its moth.

Fig trees exclude most or all potential pollinators other than its own species of pollinating wasp by the peculiarities of the "ostiole" which gives access to its syconium (CORNER 1988, p. 525; JANZEN 1979). When a syconium is ready for pollination, it calls forth the appropriate species of pollinator wasp by what appears to be a very species-specific odor (WEST & HERRE 1994). This wasp is uniquely equipped to penetrate the ostioles of "its" fig, which excludes other insects. Thus these fig trees depend on its pollinating wasps for its own reproduction. A pollinating wasp *could* produce more offspring than its fellows if it could lay an egg on every fig seed. After all, fig wasps are descended, instincts and all, from seed predators (WIEBES 1979). Fig trees, however, protect about half their seeds from wasp-laid eggs by means as yet unknown (WEST &

HERRE 1994). Are there other mutualisms which are "characterized by the dominance of the partner that provides resources and has a direct self-interest in the reproduction of both partners (WEST & HERRE 1994) ?

ii. Social Contracts.— Paper wasps, *Polistes fuscatus*, benefit by joining together in pairs to found a nest (REEVES & NONACS 1992). Before the first crop of workers appears, the presence of a second wasp reduces the chance that the nest is usurped, and the risk to either wasp's offspring from the death of their mother. Even though one queen establishes dominance over the other, it pays the dominant to allow the subordinate some eggs destined to become reproductives: this reduces the chance that the subordinate will fight "all out" to control the nest. If the dominant eats too many of those of the subordinate's eggs destined to become reproductives (rather than workers), or if an experimenter removes too many of these eggs, the subordinate becomes more aggressive, increasing the risk of a fight which might damage the dominant and which would certainly deprive her of her helper (REEVES & NONACS 1992).

THE IMPACT OF MUTUALISM ON ECOLOGICAL COMMUNITIES

The effects of mutualisms on ecological communities are many and profound. All "primitive" lines of vascular plants take nutrients up from the soil more effectively if their roots are infected by vesicular-arbuscular mycorrhizae (ALLEN 1993). The lineage of vesicular-arbuscular mycorrhizae dates back to when plants invaded the land (REMY *et al.* 1994): indeed, infection by ancestral mycorrhizae may have facilitated this invasion (SIMON *et al.* 1993).

Similarly, reef-building corals all possess symbiotic photosynthetic dinoflagellates (TRENCH 1987). "Carnivorous" plants such as pitcherplants (*Nepenthes*, *Sarracenia*, *Cephalotes*) and sundews (*Drosera*) derive their energy from photosynthesis, but obtain their nutrients by trapping insects (GIVNISH 1988). By incorporating zooxanthellae and becoming the marine equivalent of pitcherplants, reef-building corals have achieved remarkable dominance in nutrient-poor waters (TRENCH 1987).

MUTUALISMS AND THE DIVERSITY OF TROPICAL FOREST

Mutualisms have played an equally important rôle in the evolution and diversification of terrestrial plants (CORNER 1964, pp. 184-185). In the early Cretaceous, pollen-eating insects were already pollinating plants (CREPET *et al.* 1991). In the middle or late Cretaceous, some angiosperms began using nectar to attract animals, primarily insects, to serve as relatively species-specific

pollinators (CREPET *et al.* 1991, 1992, NIXON & CREPET 1993). Instead of scattering pollen at random and wasting vast quantities of it, these angiosperms used insects to convey pollen to a conspecific flower. This event triggered an explosive diversification among flowering plants (CREPET 1984, WING *et al.* 1993). In the early Cenozoic, flowering plants "domesticated" animals to serve them as seed dispersers (TIFFNEY 1984). Rewarding animals for dispersing seeds sparked adaptive radiations in many groups of birds and mammals (SUSSMAN 1991). Using mammals, which can carry large seeds, suitable for shade-tolerant species, far from their parent (REGAL 1977, SUSSMAN 1991), allowed flowering plants to dominate mature forest (TIFFNEY 1984); they had not yet done so before the Cretaceous ended, despite their diversity (WING *et al.* 1993). Using animals as pollinators and seed dispersers allowed species of mature forest tree to persist when rare.

At the end of the Jurassic and the beginning of the Cretaceous, land vegetation must have been remarkably loaded with anti-herbivore toxins. Reptilian herbivores can eat food whose tannin content is high enough to deter mammals, and the vertebrate herbivore fauna of the time was dominated by giant dinosaurs, "walking compost heaps" (COE *et al.* 1987).

Yet pathogens and insect pests seem to be the primary influence on a vegetation's load of toxins, and species which can persist when rare need invest less in defences against these plagues. Rare species can use relatively inexpensive compounds such as alkaloids, low concentrations of which suffice to deter generalist pests, as anti-herbivore defenses (COLEY *et al.* 1985). Specialized pests can penetrate such defenses, but these pests are presumably genus- or species-specific because the machinery needed to penetrate one such defense apparently precludes the ability to penetrate others. Such specialists disperse much less successfully from one plant to another when their host species is rare (GILLETT 1962). Individuals of rare species, being less burdened with the costs of defense, can devote more resources to growth and reproduction. Thus rare species can invade stands of common species whose growth is slowed by heavy investment in defense against pests. Reduced costs of defense, made possible by employing animals as pollinators and seed dispersers, apparently allowed rare angiosperms to keep invading low-diversity stands of gymnosperms, until these stands were replaced by diverse angiosperm forest (CORNER 1964, REGAL 1977), whose trees grew quickly and rotted quickly once dead. In sum: angiosperms have prevailed because "the flowering plant has developed the strategy that employs animals in its prime needs of pollination and seed dispersal, and in the processing of vegetable excess into manure." (CORNER 1964, p. 185).

Herbivore pressure favors other mutualisms, some of which further enhance tree diversity. Many plants secrete nectar (SCHUPP & FEENER 1991), and some construct more elaborate structures (JANZEN 1966, McKEY 1984, SCHUPP 1986) to attract ants which keep herbivores away. Seeds of some species must be buried by agoutis or other rodents, because insects, pathogens, and/or vertebrate herbivores destroy unburied seeds (SMYTHE 1989, FORGET & MILLERON 1991, FORGET 1993, 1994, LEIGH *et al.* 1993). Some anti-herbivore mutualisms directly enhance tree diversity. In Neotropical forest fruiting, especially of large-seeded tree species, is episodic and often infrequent, so agoutis can live only where there are enough different kinds of trees to ensure the availability of food all through the year. However well-defended its leaves, a tree species which needs agoutis to bury its seeds cannot form monospecific stands, because agoutis cannot live in them (FORGET 1994, p. 417). More generally, a tree's reproductive success fluctuates from year to year in response to the varying abundance and effectiveness of its pollinators and seed-dispersers (as well as its seed-eaters and seedling browsers). Since different tree species attract different arrays of pollinators, dispersers and pests, the variety of mutualisms in tropical forest helps to ensure that different tree species occupy disproportionately many of the new treefall gaps in different years. This "temporal sorting in recruitment" allows more tree species to coexist (CHESSON & WARNER 1981, LEIGH 1982).

Neighborhood Selection and the Luxuriance of Tropical Forest

Resorting to rarity to escape insect pests creates a selection for mutualism among forest trees. Rarity is part of the antiherbivore defense of those tree species whose pests eliminate seedlings and saplings near their parents (JANZEN 1970). Such species must disperse seeds beyond the reach of their parent's pests. Such long-distance seed dispersal creates a selection among neighborhoods (*cf.* Appendix, §5). A tree competes with a few near neighbors for the light, water and nutrients needed to grow and reproduce, but its seeds disperse far beyond the neighborhood of their parent's competitors, thereby superposing a reproductive competition among neighborhoods upon the competition within neighborhoods for the resources needed for growth and reproduction (LEIGH 1994). Each neighborhood has several species of trees, so selection among neighborhoods influences interactions among species.

Neighborhood selection favors adaptations which improve the soil or otherwise assist neighbors as well as the agent. Such adaptations help the agent produce more young without intensifying the competition these young face, for the agent's young are competing primarily with young whose parents are far beyond the reach of the

agent's benefits. Similarly, neighborhood selection discriminates against "spiteful" agents who sacrifice some of their own reproduction to annihilate competitors of other species. Neighborhood selection only works, however, when seeds disperse further than the spite propagates. In the "pine barrens" of New Jersey (GIVNISH 1981), fire-resistant pines produce inflammable trash which fuels fires that kill competing oaks and ruin the soil. Selection favors this form of spite (BOND & MIDGLEY 1995) because fires spread much further than an individual tree's seeds.

How might neighborhood selection affect a forest? Often, a plant's solution to a problem affects its neighbors as well as itself (LEIGH 1994). Some plants depend for their nutrient uptake on vesicular-arbuscular mycorrhizae, which seedlings of most other species can acquire by root contact; others employ ectomycorrhizae, many of which only conspecific seedlings can share (JANOS 1980). The leaves of some plants decay readily when they fall, improving the soil; the leaves of other plants are full of long-lived poisons which block their decomposition when they fall, and decrease soil quality (HOBBIE 1992). Some plants favor earthworms and otherwise improve the physical qualities of their soil in ways which benefit neighbors (JOFFRE & RAMBAL 1988). Some plants lift water from the subsoil, which becomes available to neighbors (DAWSON 1993). A plant may deploy roots and leaves in a manner which enhances its whole neighborhood's productivity, or in a way which enhances its own competitive ability at the expense of its neighbors (HORN 1971, KING 1993). Some plants form root grafts with neighbors which enables all the plants so grafted to resist windthrow by hurricanes (BASNET *et al.* 1993). Long-distance seed dispersal presumably allows neighborhood selection to tip the balance in favor of solutions more favorable to neighbors.

How can we assess the impact of neighborhood selection? One approach is to compare a mixed rainforest whose trees have well-dispersed seeds with an adjacent "single-dominant" rainforest dominated by a species of tree whose seeds rarely disperse beyond their parents' crowns (CONNELL & LOWMAN 1989). Following HART *et al.* (1989), LEIGH (1991, 1994) compared forest whose canopy consists entirely of the caesalpinoid legume *Gilbertiodendron dewevrei* whose large, heavy seeds simply fall to the ground under their parent (HART 1990) and adjoining diverse rain forest whose trees have well-dispersed seeds. As theory suggests, *Gilbertiodendron dewevrei* employs ectomycorrhizae, presumably species-specific, while vesicular-arbuscular mycorrhizae prevail in the surrounding mixed forest (FASSI & MOSER 1991). *Gilbertiodendron* trees drop a thick decay-resistant litter which reduces herbaceous cover, and the even canopy of *Gilbertiodendron* forest lets through far less light than the

uneven canopy of adjacent mixed forest (HART 1990, FASSI & MOSER 1991). This comparison is not decisive: we need experimental studies comparing seedling and sapling regeneration in *Gilbertiodendron* forest and adjacent mixed forest, and comprehensive contrasts of other monodominant forests with adjacent mixed forests. Nonetheless, it appears that neighborhood selection favors a more dynamic forest, which is much richer in animals (LEIGH 1994).

Fig Trees and a Replay of the Origin of Angiosperms

Fig trees have taken species-specific pollination and long-distance seed dispersal one step further. Each species of fig tree has its own species of pollinating wasp (CORNER 1940), inherited from its ancestors: figs and their pollinating wasps diversify in parallel (E. A. HERRE, personal communication). Most species of fig tree bear their fruit in synchrony, so that a fertilized wasp just emerging from a fruit cannot find another fruit to pollinate on the same tree (JANZEN 1979). Even rare species of fig tree can maintain extraordinarily high levels of genetic variation (HAMRICK & MURAWSKI 1991): their wasps must fly far to find trees to pollinate. In Panamá, 28 fruits collected from a single fruit crop of a strangler fig, *Ficus obtusifolia*, were pollinated by wasps from 22 different paternal trees (J. NASON, E. A. HERRE and J. HAMRICK, ms.). Mature forest on Barro Colorado Island, Panamá, has roughly one adult *Ficus obtusifolia* per six hectares. As less than one in twenty adult trees would be releasing fertilized wasps when these 28 fruits needed pollinators, this *Ficus obtusifolia* must have attracted pollinators from over 2500 hectares of mature forest. A fig wasp is minute: a single fig seed provides enough food to make one. Yet they are extraordinarily effective long-distance pollinators.

In the Neotropics, fig seeds are dispersed primarily by bats. When feeding, these bats all remove fruits some distance away from the parent tree before eating them (MORRISON 1978a, HOWE 1979), for fear of the predators that lurk in fruiting trees, waiting for unwary frugivores (KALKO *et al.* 1995). Some of these bats fly several kilometers in search of trees bearing ripe figs (MORRISON 1978a, 1978b). These bats are accordingly effective seed dispersers, which must carry some seeds remarkably long distances.

Fig trees pay heavily for effective pollination. As a fertilized female wasp must find figs to pollinate within the few days before she dies, most species of fig have some trees with figs ready to pollinate at any given time of year (MILTON *et al.* 1982, WINDSOR *et al.* 1989). Consequently, there are figs ready to eat all through the year, regardless of the propitiousness of the season for fig reproduction (MILTON *et al.* 1982, WINDSOR *et al.* 1989). Moreover, figs with larger fruits are apparently "paying

extra" for more effective seed dispersal. Fig wasps are killed by relatively slight overheating: larger fig fruits must transpire precious water to keep their wasps cool enough (PATIÑO *et al.* 1994). Larger fig fruits are also pollinated by more wasps per fruit (HERRE 1993). Where the foundress number N of wasps pollinating each fruit is larger, the proportion of males among their offspring is higher, wasting more of the fig tree's resources on useless non-pollinators (HERRE 1989). Moreover, where more wasps pollinate each fig fruit, the nematodes parasitizing these wasps are more virulent (HERRE 1993). Apparently, the only *advantage* of larger fig fruits (PATIÑO *et al.* 1994) is that they attract larger bats (BONACCORSO 1979), which fly further (KALKO *et al.* 1995).

Fig trees appear to stand in much the same relation to other angiosperms that the early angiosperms did to gymnosperms. Fig trees grow quickly (JANZEN 1979). *Ficus insipida* photosynthesizes as rapidly per unit area of leaf as crop plants, and much more rapidly than any other species of tree recorded in the literature (ZOTZ *et al.* 1995). "By leaf, fruit and easily rotted wood fig-plants supply an abundance of surplus produce." (CORNER 1967, p. 24). Indeed, in many areas, figs are a resource of central importance. To maintain their pollinators, most species of fig tree must supply ripe fruit all year long. In Asia and the Neotropics, figs are therefore a "keystone resource" whose availability animals can rely on during a season of food shortage (TERBORGH 1986). On Barro Colorado, figs are so steady and reliable a source of fruit that they provide the staple food for a guild of bats specializing on canopy fruit (BONACCORSO 1979) which includes 10 of the island's 20 species of fruit-eating bat (KALKO *et al.* 1995). On that island, fig fruit and nitrogen-rich fig leaves are a major resource for howling monkeys (MILTON 1980) while the small red "bird-figs" of four additional strangler species feed a variety of birds (KALKO *et al.* 1995). The rotting wood of *Ficus insipida* supports an extraordinarily diverse and busy community of insects and other arthropods (ZEH & ZEH 1991, 1992, 1994). Just as angiosperms grew faster, bore tastier and more abundant fruit and leaves, and were more putrescible than gymnosperms, so figs grow faster, provide better food more reliably, and rot more readily once dead, than most angiosperms. More effective pollination, centering on refining the mutualism with insects, triggered each advance. In both cases, improvement in the pollinator mutualism enhanced the luxuriance, and the degree of mutualism, in the forest as a whole. The evolution of tropical rain forest is perhaps the best-documented evidence of the seemingly autocatalytic rôle of mutualism in the organization and evolution of ecological communities.

APPENDIX: THE VARIETIES OF "GROUP SELECTION"

1. THE CRUCIAL ROLE OF VARIANCE WITHIN AND AMONG SUBPOPULATIONS

Consider the change ΔZ in a population's mean value Z of a quantitative variate z between generations t and $t + 1$. Let this population consist of n subpopulations. Following the Appendix of FRANK (1994), let $q_i(t)$ be the proportion of the population which belongs to subpopulation i at generation t ; let $Z_i(t)$ be the mean value of z in subpopulation i at this time; let $q_i(t + 1)$ be the proportion of the population's adults in generation $t + 1$ with parents in subpopulation i (an individual with only one parent in subpopulation i counts as $1/2$); and let the mean value of z among these offspring be $Z_i(t + 1)$. Then

$$\Delta Z = \sum_{i=1}^n q_i(t+1)Z_i(t+1) - \sum_{i=1}^n q_i(t)Z_i(t) \quad (2)$$

Let w_i be the average number of offspring per parent contributed by subpopulation i to generation $t + 1$, and W the average number of offspring in generation $t + 1$ per parent in generation t for the population as a whole. Then

$$\begin{aligned} q_i(t+1) &= q_i(t) \frac{w_i}{W}; \\ q_i(t+1) - q_i(t) &= q_i(t) \frac{w_i - W}{W} \end{aligned} \quad (3)$$

Let $Z_i(t+1) = Z_i(t) + \Delta Z_i$, where ΔZ_i is the change in the mean value of z between members of subpopulation i in generation t and their offspring in generation $t + 1$. Then

$$\Delta Z = \sum_{i=1}^n Z_i[t_i(t+1) - q_i(t)] + \sum_{i=1}^n q_i(t+1)\Delta Z_i \quad (4)$$

$$\Delta Z = \sum_{i=1}^n q_i(t)Z_i(t) \frac{w_i - W}{W} + \sum_{i=1}^n q_i(t)\Delta Z_i \frac{w_i}{W} \quad (5)$$

$$\Delta Z = \frac{1}{W} [\text{cov}(w_i, Z_i) + \sum_{i=1}^n w_i q_i(t) \Delta Z_i] \quad (6)$$

The regression $\Delta w_i / \Delta Z_i$ of a subpopulation's fitness w_i on its mean value Z_i of z can be expressed as $\text{cov}(w_i, Z_i) / V_b(Z_i)$, where $V_b(Z_i)$ is variance among the subpopulations' mean values of z . Setting $\Delta w_i / W \Delta Z_i = d \log w_i / d Z_i$, the proportionate increase of a subpopulation's fitness occasioned by a unit increase in its average z , we find selection among subpopulations contributes an amount

$$\frac{1}{W} \text{cov}(w_i, Z_i) = V_b(z) \frac{d \log w_i}{d Z_i} \quad (7)$$

to the change ΔZ in the population's mean value of z . This contribution is the variance among subpopulations in mean z , times the intensity of selection among subpopulations on their average values of z .

Now suppose that the change ΔZ_i in the mean value of z between the members of subpopulation i at generation t and their adult offspring arises only from changes in gene frequency, not from changes in a given genotype's expected value of z . Reasoning as for equation 5, but setting $\Delta z = 0$ suggests that

$$\Delta Z_i = \frac{1}{w_i} \text{cov}_i(w, z) = V_i(z) \frac{d \log w}{dz} \quad (8)$$

Here, $\text{cov}_i(w, z)$ is the covariance of w and z in subpopulation i , $V_i(z)$ is the variance in z within subpopulation i , and $d \log w / dz$ is the expected proportionate increase in an individual's proportional share of its population's reproduction from a unit increase in z . CROW & NAGYLAKI (1976) find that equation 7 is true, provided that

1. We estimate a genotype's fitness from the average fitness of its component alleles. For example, consider a locus where the genotypes **AA**, **Aa** and **aa** have frequencies q^2 , $2q(1 - q)$ and $(1 - q)^2$, and produce w_{AA} , w_{Aa} and w_{aa} offspring per parent respectively. Here, the average fitnesses - what FISHER (1958) called the average excess in fitness, of the alleles **A** and **a** are $w_A = q w_{AA} + (1 - q) w_{Aa}$ and $w_a = q w_{Aa} + (1 - q) w_{aa}$. To calculate the desired covariance, we assign **AA**, **Aa** and **aa** the relative fitnesses w_A^2 , $w_A w_a$ and w_a^2 respectively: these may differ greatly from the expected numbers of offspring w_{AA} , w_{Aa} and w_{aa} produced by **AA**, **Aa** and **aa** parents.

2. The other covariate is an individual's "additive genetic z " obtained by adding to the population mean Z , the "average effect" (FISHER 1958) on z from each allele present in the genotype. Thus $\text{cov}(w, z)$ is the covariance between the average effect on z of an individual's genotype, and that genotype's average excess in fitness, as calculated from its component alleles (CROW & NAGYLAKI 1976), and $V_i(z)$ is subpopulation i 's average genetic variance in z . With this proviso, we may express the change in the population's grand mean Z over one generation as

$$\Delta Z = V_b(Z_i) \frac{d \log w_i}{d Z_i} + \sum_{i=1}^n q_i(t) V_i(z) \frac{d \log w}{dz} \quad (9)$$

the variance $V_b(Z_i)$ in mean z among subpopulations, times the intensity of selection among subpopulations, plus the average over all subpopulations of within population additive genetic variance, multiplied by intensity of selection on z within subpopulations.

Let us now flesh out these remarks in detail. To calculate ΔZ_i , assume first that z is affected by a single locus with alleles A and a . Let the frequencies of AA , Aa and aa in subpopulation i at generation t be q^2 , $2q(1-q)$ and $(1-q)^2$, and let the average z 's for these genotypes be z_{AA} , z_{Aa} and z_{aa} respectively. If the subpopulation's adult offspring are also in Hardy-Weinberg equilibrium, and if the change in A 's frequency from parents to adult offspring is dq , then

$$\Delta Z_i = 2z_{AA}dq + 2z_{Aa}(1-2q)dq - 2z_{aa}(1-q)dq \quad (10)$$

The average z values for A and a bearers respectively, counting homozygotes as whole individuals and heterozygotes as half-individuals in each case, are $z_A = qz_{AA} + (1-q)z_{Aa}$ and $z_a = qz_{Aa} + (1-q)z_{aa}$. Now let $a = q(z_{AA} - z_{Aa}) + (1-q)(z_{Aa} - z_{aa})$. This is the average effect on an individual's z of replacing an a -allele by an A -allele (FISHER 1941). At HARDY-WEINBERG equilibrium, $a = z_A - z_a$, and $\Delta Z_i = 2adq$. Here, the average contribution a_A of a single A allele to an individual's value of z is $(1-q)\alpha = z_A - Z$, while the average contribution a_a of a single a allele is $-q\alpha = z_a - Z$. The least square estimates from a linear model of gene effects of z_{AA} , z_{Aa} and z_{aa} , the "additive genetic z " of AA , Aa and aa , are $Z + 2(1-q)\alpha$, $Z + (1-2q)\alpha$, and $Z - 2q\alpha$ respectively. Replacing z_{AA} , z_{Aa} and z_{aa} by their linear estimates, $Z + 2\alpha_A$, $Z + \alpha_A + \alpha_a$, and $Z + 2\alpha_a$, in the expression for ΔZ_i does not affect its value: notice that

$$\Delta Z_i = 2\alpha_A d(q^2) + 2(\alpha_A + \alpha_a)d[q(1-q)] + 2\alpha_a d(1-q)^2 = 2(\alpha_A - \alpha_a)dq = 2\alpha dq \quad (11)$$

If we set

$$\begin{aligned} Wdq &= (w_A - W)q; \\ Wd(1-q) &= (w_a - W)(1-q), \end{aligned} \quad (12)$$

then

$$\begin{aligned} Wd(q^2) &= 2(w_A - W)q^2; \\ Wd[q(1-q)] &= (w_A + w_a - 2W)q(1-q); \\ Wd(1-q)^2 &= 2(w_a - W)(1-q)^2 \end{aligned} \quad (13)$$

Notice that the change in AA 's frequency is governed by a double dose of the average excess in fitness of the allele A : the change is decided by w_A , not w_{AA} . ΔZ_i may accordingly be expressed as

$$\begin{aligned} & q^2(2\alpha_A)2(w_A - W) + 2q(1-q)(\alpha_A + \alpha_a)(w_A + w_a - 2W) + \\ & (1-q)^2(2\alpha_a)2(w_a - W) \end{aligned} \quad (14)$$

this expression is $\text{cov}(\alpha, w)$... the covariance between a genotype's "additive genetic z " and its average excess in fitness as inferred from its component alleles (CROW & NAGYLAKI 1976). Again, we express $\text{cov}(\alpha, w)/w$ as $V_i(z)d \log w/dz$, where $V_i(z)$ is the additive genetic variance in z , the variance in additive genetic z . If we express α_A and α_a in terms of α , $V_i(z)$ becomes

$$\begin{aligned} & q^2[2(1-q)\alpha]^2 + 2q(1-q)[(1-2q)\alpha]^2 + (1-q)^2(2q\alpha)^2 = \\ & 2q(1-q)\alpha^2 \end{aligned} \quad (15)$$

The additive genetic variance in z is α^2 times the proportion of heterozygotes in the population.

If z is affected by several loci in linkage equilibrium, $\text{cov}(\alpha, w)$ can be obtained by adding the covariances for each locus. " $d \log W/dZ$ " is now $1/W$ times the regression of the multivariate additive genetic z on genotypic average excess in fitness.

2. Converting Within- to Among-Population Variance

The relative impact on ΔZ of selection within and among subpopulations hinges on the relative magnitudes of $V_b(Z_i)$, the variance among subpopulations in mean z , and the average additive genetic variance in z within subpopulations, $v(z)$. As we shall see, the relative magnitudes of $V_b(Z_i)$ and $v(z)$ are set by the degree of gene exchange among subpopulations. Reducing gene exchange increases $V_b(Z_i)$. If individuals tend to mate with members of their own subpopulation, then population-wide heterozygosity is less, by a factor we call $1-F$, than if mating were random. Then the frequencies of AA , Aa and aa in the population as a whole are $q^2(1-F) + qF$, $2q(1-q)(1-F)$ and $(1-q)^2(1-F) + (1-q)F$ respectively, and the variance $V_i(z)$ in the population as a whole is

$$\begin{aligned} & Fq[2\alpha(1-q)]^2 + F(1-q)(2\alpha q)^2 + (1-F)2\alpha^2 q(1-q) = \\ & (1+F)2\alpha^2 q(1-q) \end{aligned} \quad (16)$$

The average proportion of heterozygotes within subpopulations is that within the population as a whole: if mating within subpopulations is random, variance within subpopulations $V_i(z)$ must average $2\alpha^2 q(1-q)(1-F)$. Variance among subpopulations, $V_b(Z_i) = V_T(z) - v(z)$, is therefore $2F\alpha^2 q(1-q)$. Thus a breeding pattern which reduced within-population variance by $F\alpha^2 q(1-q)$

created twice this amount in among-population variance (WRIGHT 1951, Appendix C). In general, converting within population variance to among-population variance doubles the variance so converted, whereas the reverse transition halves it.

3. Kin Selection, Individual Advantage, and the Group's Good

Let us now suppose, with SLATKIN & WADE (1978), that all subpopulations have N adults apiece, and that the additive genetic variance in $\mathbf{z}$ is the same, say $v(\mathbf{z})$, for each. First, selection among subpopulations can be shown to be a species of kin selection (HAMILTON 1964). A population's total variance V_T is $v(\mathbf{z}) + V_b(\mathbf{Z}_i)$, the sum of within- and between-subpopulation variance, so the intraclass correlation coefficient among members of the same subpopulation is $r = V_b(\mathbf{Z}_i)/V_T$. If we represent $d\log w/d\mathbf{z} = -c$ as the cost to an individual of a unit increase in an altruistic trait, and $d\log w_i/d\mathbf{Z} = b - c$ as the net benefit to a subpopulation of a unit increase in its mean value of the trait, then we may rewrite equation 9 as $\Delta\mathbf{Z} = r V_T(b - c) - (1 - r)c V_T$. $\mathbf{Z}$ increases if $br > c$, that is to say, if the relatedness of an altruistic individual to its fellow group members r , times the benefit b to these members of the altruism, exceeds the cost to the individual of the altruistic trait (CROW & AOKI 1982).

Next, let us consider relatively long-lived populations, and ask what circumstances allow enough variance among populations to favor a subpopulation's good over the advantage of its individuals. Suppose first that our subpopulations are immortal, and that a proportion m of the population's individuals are exchanged as migrants among subpopulations each generation. Each generation, the sampling of one generation's adults from the preceding generation's gametes adds $v(\mathbf{z})/N$ to the variance among populations (LANDE, 1976b) while, on the average, migrants reduce the difference between a subpopulation's mean value of $\mathbf{z}$ and the population's grand mean, $\mathbf{Z}_i - \mathbf{Z}$, by a factor $1 - m$. Migrants thus multiply variance among subpopulations by $(1 - m)^2 = 1 - 2m$ each generation. Thus the influence of migration and genetic drift on $V_b(\mathbf{z})$ balance when

$$\begin{aligned} 2mV_b(\mathbf{Z}_i) &= \frac{v(\mathbf{z})}{N}; \\ 2mNV_b(\mathbf{Z}_i) &= v(\mathbf{z}) \end{aligned} \quad (17)$$

(cf. LANDE 1992, equation 5a). Many have concluded that a benefit to the group balances an equally great advantage to one of its individuals when $2mN = 1$ and $V_b(\mathbf{Z}_i) = v(\mathbf{z})$ (CROW & AOKI 1982, LEIGH 1983). Migration between subpopulations must be minimal if the good of the fellow members in an individual's subpopulation is to make any difference in his behavior.

4. When Does Selection Among Populations Dominate Evolution?

The "good of the subpopulation" takes on more concrete meaning when subpopulations themselves die and reproduce. Suppose that $1/L$ of the population's n subpopulations die at the end of each individual generation, and that each subpopulation is immediately replaced by a colony of K young from one of the surviving subpopulations (in the next generation, the new subpopulation's size rises to N). During one individual generation, the $(1 - 1/L)$ surviving populations experience migration and genetic drift, which influence their variance as before, while the remaining fraction $1/L$ of the subpopulations which died are replaced by colonies from other subpopulations. Following LANDE (1992), the variance among populations in generation $t + 1$ may be expressed

$$\left(1 - \frac{1}{L}\right) \left[V_b(\mathbf{Z}_i)(1 - 2m) + \frac{v(\mathbf{z})}{N} \right] + \frac{1}{L} [V_c(\mathbf{Z}_i)] \quad (18)$$

as where the new populations are sampled from a pool with variance among means of $V_b(\mathbf{Z}_i)$. We may express $V_c(\mathbf{Z}_i)$ as $v(\mathbf{z})/K + V_b(\mathbf{Z}_i)(1 - 2/n)$, where the first term reflects the influence of within-population variance on means of samples of K individuals from the available colonists, and the second term reflects the variance arising from the fact that each new subpopulation arises from a parent, chosen at random. The chances of which subpopulations die and which are chosen to "reproduce" reduces the contribution of among-population variance by a factor of $1 - 2/n$ (LEIGH *et al.* 1993, equation 5): this reduction is the among-population analogue of the depletion of the variance of isolated populations by genetic drift. $V_b(\mathbf{Z}_i)$ is therefore in balance when

$$\left[\frac{v(\mathbf{z})}{N} - 2mV_b(\mathbf{Z}_i) \right] \left(1 - \frac{1}{L} \right) + \frac{1}{L} \left[\frac{v(\mathbf{z})}{K} - V_b(\mathbf{Z}_i) \left(\frac{2}{n} \right) \right] = 0 \quad (19)$$

$$\frac{v(\mathbf{z})}{N} \left(1 - \frac{1}{L} \right) + \frac{1}{L} \frac{v(\mathbf{z})}{K} = 2mV_b(\mathbf{Z}_i) \left(1 - \frac{1}{L} \right) + \frac{2V_b(\mathbf{Z}_i)}{nL} \quad (20)$$

Now set $(1 - 1/L)/N + 1/LK = 1/N_e$. N_e is the "effective population size" (CROW & KIMURA 1970), the harmonic mean of a subpopulation's size over the L generations of its expected life. If $m = 0$, $V_b(\mathbf{Z}_i)$ is in balance when $v(\mathbf{z})/N_e = 2V_b(\mathbf{Z}_i)/nL$. The intensity of selection is best measured by the proportionate increase in an entity's lifetime fitness. Thus selection within and among populations is equally intense when the fitness change per individual per individual lifetime is the same as the fitness change per population per population lifetime (LEIGH

1983). Thus $V_b(\mathbf{Z}_i)$ must equal $Lv(\mathbf{z})$ for selection among subpopulations to meet selection within subpopulations on equal terms. This occurs when $2n = N_e$: that is to say, when there are twice as many populations as individuals per population.

Similarly, if there is migration among populations, while the number n of subpopulations is so large that we may safely set $2/n = 0$, then $V_b(\mathbf{Z}_i)$ is in balance when

$$\begin{aligned} \frac{v(\mathbf{z})}{N_e} &= 2mV_b(\mathbf{Z}_i)\left(1 - \frac{1}{L}\right); \\ \frac{V_b(\mathbf{Z}_i)}{L} &\approx \frac{v(\mathbf{z})}{2mN_eL} \end{aligned} \quad (21)$$

Selection among populations meets selection within populations on equal terms if $2mN_eL \approx 1$, that is to say, if one migrant is exchanged per every two populations per population lifetime.

Yet another condition, so far implicitly assumed, must also be met to ensure the prevalence of selection among subpopulations. Let there be infinitely many subpopulations, which exchange no migrants, a fraction $1/L$ of which die at the end of each generation. When a population dies, it is replaced by K adults chosen at random from the surplus young of k different islands (up to now, we have set $k = 1$). If among population variance is $V_b(\mathbf{Z}_i)$ in generation t , then in generation $t + 1$ it will be

$$\left[V_b(\mathbf{Z}_i) + \frac{v(\mathbf{z})}{N}\right]\left(1 - \frac{1}{L}\right) + \frac{1}{L}[V_c(\mathbf{z})] \quad (22)$$

Here, the genetic variance $V_c(\mathbf{Z}_i)$ among newly established populations is the variance among means of samples of k population means, $V_b(\mathbf{Z}_i)/k$, plus variance in means of samples of K from the pool of colonists available to replace a given population, σ_c^2/K . The additive genetic variance σ_c^2 in the pool of potential colonists is the heritable variance within a population, plus $1/2$ the variance in a sample of k population means (recall that converting among- to within-population variance halves it). Thus

$$\sigma_c^2 = v(\mathbf{z}) + \frac{1}{2}\left(1 - \frac{1}{k}\right)V_b(\mathbf{z}) \quad (23)$$

$$V_c(\mathbf{z}) = \frac{V_b(\mathbf{z})}{k} + \frac{1}{K}\left[v(\mathbf{z}) + \frac{1}{2}\left(1 - \frac{1}{k}\right)V_b(\mathbf{z})\right] \quad (24)$$

Gain of variance from genetic drift balances loss from replacing established by newly colonized populations when

$$\left(1 - \frac{1}{L}\right)\frac{v(\mathbf{z})}{N} = \frac{1}{L}\left\{\left[V_b(\mathbf{z}) - \frac{V_b(\mathbf{z})}{k}\right] - \frac{1}{K}\left[v(\mathbf{z}) + \frac{1}{2}\left(1 - \frac{1}{k}\right)V_b(\mathbf{z})\right]\right\} \quad (25)$$

$$\left(1 - \frac{1}{L}\right)\frac{v(\mathbf{z})}{N} + \frac{1}{L}\frac{v(\mathbf{z})}{K} = \frac{1}{L}\left[V_b(\mathbf{z})\left(1 - \frac{1}{k}\right)\left(1 - \frac{1}{2K}\right)\right] \quad (26)$$

As before, set $(1 - 1/L)/N + 1/LK = 1/N_e$, where N_e is the average population's lifetime harmonic mean number of adults. If $2K \gg k$, $V_b(\mathbf{z})$ equilibrates when

$$\frac{v(\mathbf{z})}{N_e} \approx \frac{1}{L}V_b(\mathbf{z})\left(1 - \frac{1}{k}\right) \quad (27)$$

(LANDE 1992, equation 8a, with $m = 0$). Here, selection among subpopulations balances selection among individuals within subpopulations when $N_e(1 - 1/k) = 1$, $k = N_e/(N_e - 1)$. Nearly every population must descend from a single pre-existing population if selection among populations is to dominate selection within populations (LEIGH 1983).

In sum, selection among subpopulations can only dominate selection within subpopulations if there are many more subpopulations than individuals per population, almost no migrants are exchanged among subpopulations, and nearly every subpopulation derives from a single preexisting population.

5. Traitgroup and Neighborhood Selection

Finally, let us consider a population whose individuals aggregate in trait-groups of N adults apiece, but disperse their young into a common pool, from which the next generation's traitgroups are sampled at random (WILSON 1975, 1980). It seems rather farfetched to consider these traitgroups as reproductive individuals in their own right: they have too many "parents", and boundary between one and the next is often too undefinable, for such an analogy to be meaningful. Yet this kind of population organization may have important consequences (WILSON 1980). Let us express an individual's "additive genetic $\mathbf{z}$ " as the population mean $\mathbf{Z}$, plus the average effect on $\mathbf{z}$ of each of that individual's genes. Then the variance among a traitgroup's members in additive genetic $\mathbf{z}$ is $V(1 - 1/N)$, the variance among a sample of N from a population whose variance among individuals in additive genetic $\mathbf{z}$ is V . Similarly, the variance among traitgroups in their mean values of (additive genetic) $\mathbf{z}$ is V/N . Here, group advantage has only $1/(N - 1)$ times the influence of equally intense individual advantage on the evolution of $\mathbf{Z}$. The same result obtains if the population is continuously distributed, with each individual's reproduction governed by its interaction with $N - 1$ fixed neighbors (WILSON 1975), or if individuals in this continuous population die one by one, rather than whole generations together (LEIGH 1991).

First, let us consider a population with discrete trait-groups. Consider a species of fig tree where N fertilized female wasps enter each "syconium," pollinate its flowers, and lay eggs in some of them. These N fertilized "foundresses" can be considered as a "mating trait-group" whose members use the syconium to elaborate a new generation of mated females, which fly off to a common pool from which the next generation's mating trait-groups are drawn at random.

What is the joint effect of selection within and among traitgroups on the sex ratio of the offspring of these wasps? Let us suppose, for simplicity, the fiction that fig wasps are diploid (in fact, they are haplodiploid). Let sex ratio be governed by a single autosomal locus, with alleles **A** and **a**. Let all mothers produce the same number B of offspring, but let the proportion of females among the offspring of **AA**, **Aa** and **aa** mothers be $r + dr$, $r + dr/2$, and r respectively. In traitgroups where **A**'s frequency among the mothers is q , the mean proportion of females among their offspring is $r + qdr$. In traitgroups where **a**'s frequency is $1 - q$, the number w_a of maternal genes exported in fertilized daughters per **a**-gene in the mother is the expected number of her daughters, $B(r + qdr/2)$, plus the expected number of her sons, $B(1 - r - qdr/2)$ times the number of matings per son, which latter is the traitgroup's overall ratio of daughters to sons, $(r + qdr)/(1 - r - qdr)$. Thus

$$w_a = B\left(r + q\frac{dr}{2}\right) + B\left(1 - r - q\frac{dr}{2}\right)\frac{r + qdr}{1 - r - qdr} \quad (28)$$

$$w_a = B(r + qdr)\left[\frac{r + q\frac{dr}{2}}{r + qdr} + \frac{1 - r - q\frac{dr}{2}}{1 - r - qdr}\right] \quad (29)$$

Similarly,

$$w_A = B(r + qdr)\left[\frac{r + \frac{dr}{2}(1 + q)}{r + qdr} + \frac{1 - r - \frac{dr}{2}(1 + q)}{1 - r - qdr}\right] \quad (30)$$

$$w_A \approx w_a + \left[\frac{dr/2}{r} - \frac{dr/2}{1 - r}\right]Br \quad (31)$$

Substituting an **A** for an **a** in the mother increases the proportion of females among her offspring by an amount $dr/2$. This increase $\Delta r = dr/2$ increases her gene output by an amount $\Delta w = Br \Delta r(1 - 2r)/[r(1 - r)]$. Thus $d \log w/dr$, the proportionate gain in within-group fitness per unit change in r , is $\Delta w/w\Delta r \approx \Delta w/2Br\Delta r = (1 - 2r)/[2r(1 - r)]$. Meanwhile, increasing a traitgroup's proportion of female offspring by dr increases its output of fertilized daughters by the amount $NBdr$, so $d \log w_i/dr = 1/r$. Thus, if we let R

be the population-wide proportion of female offspring, R_i the proportion of offspring in traitgroup i which are female, then the mean change ΔR per generation in R is

$$\Delta R = V_b(R_i)\frac{d \log w_i}{dR_i} + v(r)\frac{d \log w}{dr} = V_b(R_i)\frac{dr}{r} + v(r)\frac{(1 - 2r)dr}{2r(1 - r)} \quad (32)$$

(cf. Equation 9 of Frank 1986 and Equation 9 in the Appendix). Here, $V_b(R_i)$ and $v(r)$ are variance among subpopulations, and variance among fertilized females within subpopulations, in sex ratio. Since the subpopulations here are traitgroups of N fertilized females apiece, $v(r) + V_T(r)(N - 1)/N$, $V_b(R_i) = V_T(r)/N$, where $V_T(r)$ is population-wide variance in r among fertilized females (FRANK 1986). Thus $v(r) = (N - 1)V_b$, and $\Delta R = 0$ when

$$\frac{1}{r} + \frac{(N - 1)(1 - 2r)}{2r(1 - r)} = 0; r = \frac{N + 1}{2N} \quad (33)$$

(TAYLOR & BULMER 1980). The smaller the number N of pollinating foundress wasps per fig fruit, the higher the proportion of females among the offspring (HAMILTON 1967, COLWELL 1981). When $N = 1$, just enough males should be born to fertilize the females. Analogous theory for haplodiploids has been developed by FRANK (1985, 1986), which agrees with theory and observations of HERRE (1985, 1987).

Now consider a hexagonal lattice of trees where the reproductive output of each tree is governed by its interactions with its six nearest neighbors, so that a "neighborhood" or traitgroup includes 7 adults, while a tree's seeds are dispersed evenly over a hexagon of radius n , which includes $3n(n - 1) + 1$ trees. Our mathematics will apply equally to genotypes within a monospecific stand of trees, and to tree species within a diverse forest. Let all trees die simultaneously, and let each tree be replaced by a seed chosen randomly from those dispersed to its site. A tree's seeds are spread over the equivalent of $[3n(n - 1) + 1]/7$ neighborhoods. The variance in mean Z_i among these M neighborhoods is presumably $(M/(M - 1))$ times what it would be were dispersal population-wide. It is therefore $(M - 1)/M(N - 1)$ times the variance in additive genetic z among the 7 individuals in a neighborhood. The effect on a locale's Z of among-group reproductive competition is reflected by the variance among just those groups which are competing to colonize that locale. If $M = 1$, group advantage has no influence on Z , while, the larger M , the more important is the rôle of group advantage (cf. BULMER & TAYLOR 1980). Trait-group selection offers no incentive for making major sacrifices for one's neighbors, but, where an organism faces a variety of different ways to solve a problem, which are

roughly equivalent from its own standpoint, but which have vastly differing impacts on neighbors, traitgroup selection favors the most "neighborly" solution.

ACKNOWLEDGEMENTS

Egbert LEIGH is most grateful to the Laboratoire d'Écologie at Brunoy for providing the opportunity to assemble our thoughts on the importance of mutualism in evolution, and to Marcel and Annette HLADIK for an overflowing abundance of kindness. Nearly every page of this paper gives evidence of Leigh's debt to Edward Allen HERRE for many helpful conversations.

Leigh is also indebted to Robert MAY, first for a very pleasant visit to Oxford just after the seminar at Brunoy, which acquainted us with the many fascinating lessons to be learned from analyses of the "iterated prisoner's dilemma," and second, for sending a reprint of a paper on a crucial stage in the origin of life. G. J. VERMEIJ asked various sharp questions which helped to clarify the paper. Finally, timely instruction by Richard CONDIT and Suzanne LOO DE LAO in the peculiarities of Macintoshes enabled me to present the equations in a mode readable by French machines.

Finally, we wish to thank the plants and animals of Barro Colorado, the monkeys of East Africa, and the many students who helped us to understand them.

REFERENCES

- ALLEN, M. F., 1993.— *The Ecology of Mycorrhizae*. Cambridge University Press, Cambridge.
- AXELROD, R., 1984.— *The Evolution of Cooperation*. Basic Books, New York.
- AXELROD, R. & W. D. HAMILTON., 1981.— The evolution of cooperation. *Science*, 211: 1390-1396.
- BASNET, K., F. N. SCATENA, G. E. LIKENS & A. E. LUGO., 1993.— Ecological consequences of root grafting in Tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. *Biotropica*, 25: 28-35.
- BIRKY, C. W. Jr., 1991.— Evolution and population genetics of organelle genes: mechanisms and models. pp. 112-134 in R. K. SELANDER, A. G. CLARK & T. S. WHITTAM, eds. *Evolution at the Molecular Level*. Sinauer Associates, Sunderland, MA.
- BOERLIJST, M. C. & P. HOGEWEG, 1991.— Spiral wave structure in pre-biotic evolution: hypercycles stable against parasites. *Physica*, D 48: 17-28.
- BONACCORSO, F. J., 1979.— Foraging and reproductive ecology in a Panamanian bat community. *Bulletin of the Florida State Museum, Biological Sciences*, 24: 359-408.
- BOND, W. J. & J. J. MIDGLEY., 1995.— Kill thy neighbor: an individualistic argument for the evolution of flammability. *Oikos*, 73: 79-85.
- BREMERMAN, H. J. & J. PICKERING., 1983.— A game-theoretic model of parasite virulence. *Journal of Theoretical Biology*, 100: 411-426.
- BULMER, M. G. & P. D. TAYLOR., 1980.— Dispersal and the sex ratio. *Nature*, 284: 448-449.
- BURDON, J. J., 1987.— *Diseases and Plant Population Biology*. Cambridge University Press, Cambridge.
- BUSS, L. W., 1987.— *The Evolution of Individuality*. Princeton University Press, Princeton NJ.
- CAMAZINE, S., 1993.— The regulation of pollen foraging by honey bees: how foragers assess the colony's need for pollen. *Behavioral Ecology and Sociobiology*, 32: 265-272.
- CHAPELA, I. H., S. A. REHNER, T. R. SCHULTZ & U. G. MUELLER., 1994.— Evolutionary history of the symbiosis between fungus-growing ants and their fungi. *Science*, 266: 1691-1694.
- CHARLESWORTH, B. & C. H. LANGLEY., 1991.— Population genetics of transposable elements in *Drosophila*. pp. 150-176 in R. K. Selander, A. G. Clark and T. S. Whittam, eds. *Evolution at the Molecular Level*. Sinauer Associates, Sunderland, MA.
- CHARNOV, E. L., 1982.— *The Theory of Sex Allocation*. Princeton University Press, Princeton NJ.
- CHESSON, P. L. & R. R. WARNER., 1981.— Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, 117: 923-943.
- CHISM, J. B. & T. E. ROWELL., 1986.— Mating and residence patterns of male patas monkeys. *Ethology*, 72: 31-39.
- CLEGG, M. T., G. H. LEARN & E. M. GOLENBERG., 1991.— Molecular evolution of chloroplast DNA. pp. 135-149 in R. K. Selander, A. G. Clark and T. S. Whittam, eds. *Evolution at the Molecular Level*. Sinauer Associates, Sunderland, MA.
- CLUTTON-BROCK, T. H., 1986.— Sex ratio variation in birds. *Ibis*, 128: 317-329.
- CLUTTON-BROCK, T. H. & G. R. IASON., 1986.— Sex ratio variation in mammals. *Quarterly Review of Biology*, 61: 339-374.
- COE, M. J., D. L. DILCHER, J. O. FARLOW, D. H. JARZEN & D. A. RUSSELL., 1987.— Dinosaurs and land plants. pp. 225-258 in E. M. Friis, W. G. Chaloner and P. R. Crane, eds. *The Origins of Angiosperms and their Biological Consequences*. Cambridge University Press, Cambridge, UK.
- COLEY, P. D., J. P. BRYANT & F. STUART CHAPIN III, 1985.— Resource availability and plant herbivore defense. *Science*, 230: 895-899.
- COLWELL, R. K., 1981.— Group selection is implicated in the evolution of female-biased sex ratios. *Nature*, 290: 401-404.
- CONNELL, J. H. & M. D. LOWMAN., 1989.— Low-diversity tropical rain forests: some possible mechanisms for their existence. *American Naturalist*, 134: 88-119.
- CONNOR, R. C., 1995.— Altruism among non-relatives: alternatives to the 'Prisoner's Dilemma'. *Trends in Ecology and Evolution* 10: 84-86.
- CORNER, E. J. H., 1940.— *Wayside Trees of Malaya*. Government Printer, Singapore.
- CORNER, E. J. H., 1964.— *The Life of Plants*. World Publishing Co., Cleveland OH.
- CORNER, E. J. H., 1967.— *Ficus in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia*. *Philosophical Transactions of the Royal Society of London B*, 253: 23-159.
- CORNER, E. J. H., 1988. *Wayside Trees of Malaya*, 3d ed. Malayan Nature Society, Kuala Lumpur.
- COSMIDES, L. M. & J. TOOBY., 1981.— Cytoplasmic inheritance and intragenomic conflict. *Journal of Theoretical Biology*, 89: 83-129.
- CREPET, W. L., 1984.— Advanced (constant) insect pollination mechanisms: pattern of evolution and implications vis-à-vis angiosperm diversity. *Annals of the Missouri Botanical Garden*, 71: 607-630.
- CREPET, W. L., E. M. FRIIS & K. C. NIXON., 1991.— Fossil evidence for the evolution of biotic pollination. *Philosophical Transactions of the Royal Society of London B*, 333: 187-195.
- CREPET, W. L., K. C. NIXON, E. M. FRIIS & J. V. FREUDENSTEIN., 1992.— Oldest fossil flowers of hamamelidaceous affinity, from the Late Cretaceous of New Jersey. *Proceedings of the National Academy of Sciences, USA* 89: 8986-8989.

- CROW, J. F., 1979.— Genes that violate Mendel's rules. *Scientific American* 240: 134-146.
- CROW, J. F., 1991.— Why is Mendelian segregation so exact? *BioEssays* 13: 305-312.
- CROW, J. F. & K. AOKI., 1982.— Group selection for a polygenic behavioral trait: a differential proliferation model. *Proceedings of the National Academy of Sciences, USA* 79: 2628-2631.
- CROW, J. F. & M. KIMURA., 1970.— *Introduction to Population Genetics Theory*. Harper and Row, New York.
- CROW, J. F. & T. NAGYLAKI., 1976.— The rate of change of a character correlated with fitness. *American Naturalist* 110: 207-213.
- DARWIN, C. R. 1859.— *The Origin of Species*. London, John Murray.
- DAWKINS, R., 1982.— *The Extended Phenotype*. Oxford University Press, Oxford.
- DAWSON, T. E., 1993.— Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. *Ecologia*, 95: 565-574.
- DYSON, F., 1985.— *Origins of Life*. Cambridge University Press, Cambridge.
- EBERHARD, W. G., 1980.— Evolutionary consequences of intracellular organelle competition. *Quarterly Review of Biology* 55: 231-249.
- EIGEN, M., W. GARDINER, P. SCHUSTER AND R. WINKLER-OSWATITCH., 1981.— The origin of genetic information. *Scientific American* 244: 88-118.
- EMLEN, S. T. & P. H. WREGE., 1992.— Parent-offspring conflict and the recruitment of helpers among bee-eaters. *Nature*, 356: 331-333.
- FASSI, B. & M. MOSER., 1991.— Mycorrhizae in the natural forests of tropical Africa and the Neotropics. pp. 157-202 in *Funghi, Pianti e Suolo*. Centro di Studio sulla Micologia del Terreno, C. N. R., Torino.
- FISCHER, E. A., 1980.— The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans* (Serranidae). *Animal Behaviour* 28: 620-633.
- FISCHER, E. A., 1981.— Sexual allocation in a simultaneously hermaphroditic coral reef fish. *American Naturalist*, 117: 64-82.
- FISCHER, E. A., 1987.— The evolution of sexual patterns in the seabasses. *BioScience*, 37: 482-489.
- FISCHER, E. A., 1988.— Simultaneous hermaphroditism, tit-for-tat, and the evolutionary stability of social systems. *Ethology and Sociobiology*, 9: 119-136.
- FISHER, R. A., 1930.— *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- FISHER, R. A., 1941.— Average excess and average effect of a gene substitution. *Annals of Eugenics* (now *Annals of Human Genetics*), 11: 53-63.
- FISHER, R. A., 1958.— *The Genetical Theory of Natural Selection*, second edition. Dover Press, New York.
- FORGET, P.-M., 1993.— Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panama. *Ecologia*, 94: 255-261.
- FORGET, P.-M., 1994.— Recruitment pattern of *Vouacapoua americana* (Caesalpinaceae), a rodent-dispersed tree species in French Guiana. *Biotropica*, 25: 408-419.
- FORGET, P.-M. & T. MILLERON., 1991.— Evidence for secondary seed dispersal by rodents in Panama. *Ecologia*, 87: 596-599.
- FRANK, S. A., 1985.— Hierarchical selection theory and sex ratios. II. On applying the theory, and a test with fig wasps. *Evolution*, 39: 949-964.
- FRANK, S. A., 1986.— Hierarchical selection theory and sex ratios. I. General solutions for structured populations. *Theoretical Population Biology* 29: 312-342.
- FRANK, S. A., 1994.— Kin selection and virulence in the evolution of protocells and parasites. *Proceedings of the Royal Society of London B*, 258: 153-161.
- FRANKS, N. R., 1989.— Army ants: a collective intelligence. *American Scientist*, 77: 138-145.
- FRANKS, N. R. & B. HÖLLDOBLER., 1987.— Sexual competition during colony reproduction in army ants. *Biological Journal of the Linnean Society*, 30: 229-243.
- GILLET, J. B., 1962.— Pest pressure, an underestimated factor in evolution. *Systematics Association Publication*, 4: 37-46.
- GIVNISH, T. J., 1981.— Serotiny, geography and fire in the pine barrens of New Jersey. *Evolution*, 35: 101-123.
- GIVNISH, T. J., 1988.— Ecology and evolution of carnivorous plants. pp. 243-290 in W. B. ABRAHAMSON, ed. *Plant-Animal Interactions*. McGraw-Hill, New York.
- GOMPPER, M., 1994.— *The Importance of Behavior, Ecology and Genetics to the Maintenance of White-nosed Coati (Nasua narica) Social Structure*. Ph. D. Dissertation, Dept. of Zoology, University of Tennessee, Knoxville.
- GRADWOHL, J. & R. GREENBERG., 1980.— The formation of antwren flocks on Barro Colorado Island, Panama. *Auk*, 97: 385-395.
- GRAY, M. W., 1983.— The bacterial ancestry of plastids and mitochondria. *BioScience*, 33: 693-699.
- HAIG, D., 1993.— Alternatives to meiosis: the unusual genetics of red algae, microsporidia, and others. *Journal of Theoretical Biology*, 163: 15-31.
- HAMILTON, W. D., 1964.— The genetical evolution of social behavior. I. *Journal of Theoretical Biology*, 7: 1-16.
- HAMILTON, W. D., 1967.— Extraordinary sex ratios. *Science*, 156: 477-488.
- HAMRICK, J. L. & D. A. MURAWSKI., 1991.— Levels of allozyme diversity in populations of uncommon Neotropical tree species. *Journal of Tropical Ecology*, 7: 395-399.
- HART, T. B., 1990.— Monospecific dominance in tropical rain forests. *Trends in Ecology and Evolution*, 5: 6-11.
- HART, T. B., J. A. HART & P. G. MURPHY., 1989.— Monodominant and species-rich forests of the humid tropics: causes for their co-occurrence. *American Naturalist*, 133: 613-633.
- HEINZE, J., B. HÖLLDOBLER & C. PEETERS., 1994.— Conflict and cooperation in ant societies. *Naturwissenschaften*, 81: 489-497.
- HERRE, E. A., 1985.— Sex ratio adjustment in fig wasps. *Science*, 228: 896-898.
- HERRE, E. A., 1987.— Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature*, 329: 627-629.
- HERRE, E. A., 1989.— Coevolution of reproductive characteristics in 12 species of New World figs and their pollinator wasps. *Experientia*, 45: 637-647.
- HERRE, E. A., 1993.— Population structure and the evolution of virulence in nematode parasites of fig wasps. *Science*, 259: 1442-1445.
- HINKLE, G., J. K. WETTERER, T. R. SCHULTZ & M. L. SOGIN., 1994.— Phylogeny of the attine ant fungi based on analysis of small subunit ribosomal RNA gene sequences. *Science*, 266: 1695-1697.
- HOBBIE, S. E., 1992.— Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution*, 7: 336-339.
- HÖLLDOBLER, B. AND E. O. WILSON. *The Ants*. Harvard

- University Press, Cambridge, MA.
- HORN, H. S., 1971.— *The Adaptive Geometry of Trees*. Princeton University Press, Princeton, NJ.
- HOWE, H. F., 1979.— Fear and frugivory. *American Naturalist*, 114: 925-931.
- HUANG, Z.-Y. & G. E. ROBINSON., 1992.— Honeybee colony integration: worker-worker interactions mediate hormonally regulated plasticity in division of labor. *Proceedings of the National Academy of Sciences, USA*, 89: 11726-11729.
- HURST, L. D., 1990.— Parasite diversity and the evolution of diploidy, multicellularity and anisogamy. *Journal of Theoretical Biology*, 144: 429-443.
- HURST, L. D., 1992.— Intragenomic conflict as an evolutionary force. *Proceedings of the Royal Society of London B*, 248: 135-140.
- HURST, L. D., 1993.— The incidences, mechanisms and evolution of cytoplasmic sex ratio distortion in animals. *Biological Reviews*, 68: 121-193.
- JANOS, D. P., 1980.— Mycorrhizae influence tropical succession. *Biotropica*, 12, supplement: 56-64.
- JANZEN, D. H., 1966.— Coevolution of mutualism between ants and acacias in Central America. *Evolution*, 20: 249-275.
- JANZEN, D. H., 1970.— Herbivores and the number of tree species in tropical forests. *American Naturalist*, 104: 501-528.
- JANZEN, D. H., 1979.— How to be a fig. *Annual Review of Ecology and Systematics*, 10: 13-51.
- JANZEN, D. H., 1980.— Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *Journal of Ecology*, 68: 929-952.
- JEON, K. W., 1972.— Development of cellular dependence on infective organisms: micrurgical studies in amoebas. *Science*, 176: 1122-1123.
- JEON, K. W., 1987.— Change of cellular "pathogens" into required cell components. *Annals of the New York Academy of Sciences*, 503: 359-371.
- JEON, K. W. & T. I. AHN., 1978.— Temperature sensitivity: a cell character determined by obligate endosymbionts in amoebas. *Science*, 202: 635-637.
- JOFFRE, R. & S. RAMBAL., 1988.— Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecologica/Oecologia Plantarum*, 9: 405-422.
- JOLLY, A., 1985.— *The Evolution of Primate Behavior*. 2d ed. Macmillan, New York.
- JONES, S. E., 1977.— Coexistence in mixed species antwren flocks. *Oikos*, 29: 366-375.
- KALKO, E. K. V., E. A. HERRE & C. O. HANDLEY Jr., 1995.— Relation of fig fruit characteristics to fruit-eating bats in the New and Old World tropics. *Journal of Biogeography*, submitted.
- KAUFMANN, J. H., 1962.— Ecology and Social behavior of the coati, *Nasua narica* on Barro Colorado Island Panama. *University of California Publications in Zoology*, 60: 95-222.
- KIMURA, M., 1965.— A stochastic model concerning the maintenance of genetic variability in quantitative characters. *Proceedings of the National Academy of Sciences, USA*, 54: 731-736.
- KING, D. A., 1993.— A model analysis of the influence of root and foliage allocation on forest production and competition between trees. *Tree Physiology*, 12: 119-135.
- KOESTLER, A., 1967. *The Ghost in the Machine*. Hutchinson Publishing Group, Ltd.
- LANDE, R., 1976a.— The maintenance of genetic variability by mutation in a polygenic character with linked loci. *Genetical Research*, 26: 221-235.
- LANDE, R., 1976b.— Natural selection and random genetic drift in phenotypic evolution. *Evolution*, 30: 314-334.
- LANDE, R., 1992. Neutral theory of quantitative genetic variance in an island model with local extinction and colonization. *Evolution*, 46: 381-389.
- LAW, R. & D. H. LEWIS., 1983.— Biotic environments and the maintenance of sex -some evidence from mutualistic symbioses. *Biological Journal of the Linnean Society*, 20: 249-276.
- LEIGH, E. G. Jr., 1970.— Sex ratio and differential mortality between the sexes. *American Naturalist*, 104: 205-210.
- LEIGH, E. G. Jr., 1971.— *Adaptation and Diversity*. San Francisco, Freeman, Cooper & Co.
- LEIGH, E. G. Jr., 1977.— How does evolution reconcile individual advantage with the good of the group? *Proceedings of the National Academy of Sciences, USA*, 74: 4542-4546.
- LEIGH, E. G. Jr., 1982.— Introduction: why are there so many kinds of tropical trees? pp. 63-66 in E. G. LEIGH, JR., A. S. RAND & D. M. WINDSOR, eds. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*. Smithsonian Institution Press, Washington, DC.
- LEIGH, E. G. Jr., 1983.— When does the good of the group override the advantage of the individual? *Proceedings of the National Academy of Sciences, USA*, 80: 2985-2989.
- LEIGH, E. G. Jr., 1987.— Ronald Fisher and the development of evolutionary theory. II. Influences of new variation on evolutionary process. *Oxford Surveys in Evolutionary Biology*, 4: 212-263.
- LEIGH, E. G. Jr., 1991.— Genes, bees and ecosystems: the evolution of a common interest among individuals. *Trends in Ecology and Evolution*, 6: 257-262.
- LEIGH, E. G. Jr., 1994.— Do insect pests promote mutualism among tropical trees? *Journal of Ecology*, 82: 677-680.
- LEIGH, E. G. Jr., E. A. HERRE & E. A. FISCHER., 1985.— Sex allocation in animals. *Experientia*, 41: 1265-1276.
- LEWONTIN, R. C., 1970.— The units of selection. *Annual Review of Ecology and Systematics*, 1: 1-18.
- LEWONTIN, R. C., 1978.— Adaptation. *Scientific American*, 239: 212-230.
- LEWONTIN, R. C. & L. C. DUNN., 1960.— The evolutionary dynamics of a polymorphism in the house mouse. *Genetics*, 45: 705-722.
- LYTTLE, T. W., 1977.— Experimental population genetics of meiotic drive systems I. Pseudo-Y chromosomal drive as a means of eliminating cage populations of *Drosophila melanogaster*. *Genetics*, 86: 413-445.
- LYTTLE, T. W., 1979.— Experimental population genetics of meiotic drive systems II. Accumulation of genetic modifiers of segregation distorter (SD) in laboratory populations. *Genetics*, 91: 339-357.
- LYTTLE, T. W., 1981.— Experimental population genetics of meiotic drive systems III. Neutralization of sex-ratio distortion in *Drosophila* through sex-chromosome aneuploidy. *Genetics*, 98: 317-334.
- MCDONALD, D. B. & W. K. POTTS., 1994.— Cooperative display and relatedness among males in a lek-mating bird. *Science*, 266: 1030-1032.
- MCKEY, D., 1984.— Interaction of the ant-plant *Leonardoxa africana* (Caesalpinaceae) with its obligate inhabitants in a rainforest in Cameroon. *Biotropica*, 16: 81-99.
- MARGULIS, L., 1981.— *Symbiosis in Cell Evolution*. W. H. Freeman, San Francisco.
- MARGULIS, L. & D. SAGAN., 1986.— *Origins of Sex*. Yale University Press, New Haven, CT.
- MAY, R. M., 1991. Hypercycles spring to life. *Nature*, 353: 607-608.

- MAY, R. M. & R. M. ANDERSON., 1983.— Epidemiology and genetics in the coevolution of parasites and hosts. *Proceedings of the Royal Society of London*, B 219 : 281-313.
- MAY, R. M. & R. M. ANDERSON., 1990.— Parasite-host coevolution. *Parasitology*, 100 : S89-S101.
- MAYNARD SMITH, J., 1978.— *The Evolution of Sex*. Cambridge University Press, Cambridge.
- MAYNARD SMITH, J., 1979.— Hypercycles and the origin of life. *Nature*, 280 : 445-446.
- MAYNARD SMITH, J., 1988.— Evolutionary progress and levels of selection. pp. 219-230 in M. H. Nitecki, ed. *Evolutionary Progress*, University of Chicago Press, Chicago, IL.
- MILTON, K., 1980.— *The Foraging Strategy of Howler Monkeys*. Columbia University Press, New York.
- MILTON, K., D. M. WINDSOR, D. W. MORRISON & M. A. ESTRIBI., 1982.— Fruiting phenologies of two Neotropical *Ficus* species. *Ecology*, 63 : 752-762.
- MORRISON, D. W., 1978a.— Foraging behavior and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology*, 59 : 716-723.
- MORRISON, D. W., 1978b.— On the optimal searching strategy for refuting predators. *American Naturalist*, 112 : 925-934.
- MOYNIHAN, M. H., 1962.— The organization and probable evolution of some mixed species flocks of Neotropical birds. *Smithsonian Miscellaneous Collections*, 143 : 1-140.
- MOYNIHAN, M. H., 1968.— Social mimicry : character convergence versus character displacement. *Evolution*, 22 : 315-331.
- MOYNIHAN, M. H., 1979.— *Geographic Variation in Social Behavior and in Adaptations to Competition among Andean Birds*. Nuttall Ornithological Club, Cambridge, MA.
- MUNN, C. A., 1985.— Permanent canopy and understory flocks in Amazonia : species composition and population density. pp. 683-712 in P. A. BUCKLEY, M. S. FOSTER, E. S. MORTON, R. S. RIDGELY & F. G. BUCKLEY, eds. *Neotropical Ornithology*. Ornithological Monographs no. 36, American Ornithologists' Union, Washington, DC.
- MUSCATINE, L., P. G. FALKOWSKI, Z. DUBINSKY, P. A. COOK AND L. R. MCCLOSKEY., 1989.— The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. *Proceedings of the Royal Society of London B*, 236 : 311-324.
- NETTING, R. McC., 1989.— Smallholders, householders, freeholders : why the family farm works well worldwide. pp. 221-242 in R. R. WILK, ed. *The Household Economy : The Domestic Mode of Production Reconsidered*. Boulder : Westview Press.
- NETTING, R. McC., 1990.— Population, permanent agriculture, and politics : unpacking the evolutionary portmanteau. pp. 21-61 in S. Upham, ed. *The Evolution of Political Systems*. Cambridge University Press, Cambridge, UK.
- NIXON, K. C. & W. L. CREPET., 1993.— Late Cretaceous fossil flowers of Ericalean affinity. *American Journal of Botany*, 80 : 616-623.
- NOWAK, M. A., S. BONHOEFFER & R. M. MAY., 1994a.— Spatial games and the maintenance of cooperation. *Proceedings of the National Academy of Sciences, USA*, 91 : 4877-4881.
- NOWAK, M. A., S. BONHOEFFER & R. M. MAY., 1994b.— More spatial games. *International Journal of Bifurcation and Chaos*, 4 : 33-56.
- NOWAK, M. A. & R. M. MAY., 1992.— Spatial games and evolutionary chaos. *Nature*, 359 : 826-829.
- NOWAK, M. A. & R. M. MAY., 1993.— The spatial dilemmas of evolution. *International Journal of Bifurcation and Chaos*, 3 : 35-78.
- Nowak, M. A. and K. Sigmund., 1992. Tit for tat in heterogeneous populations. *Nature*, 355 : 250-253.
- Nowak, M. and K. Sigmund., 1993. A strategy of win-stay, lose-shift that outperforms tit-for-tat in the Prisoner's Dilemma game. *Nature*, 364 : 56-58.
- PAGE, R. E. JR., G. E. ROBINSON & M. K. FONDRK., 1989.— Genetic specialists, kin recognition and nepotism in honey-bee colonies. *Nature*, 338 : 576-579.
- PATÍÑO, S., E. A. HERRE & M. T. TYREE., 1994.— Physiological determinants of *Ficus* fruit temperature and implications for survival of pollinator wasp species : comparative physiology through an energy budget approach. *Oecologia*, 100 : 13-20.
- PELLMYR, O. & C. J. HUTH., 1994.— Evolutionary stability of mutualism between yuccas and yucca moths. *Nature*, 372 : 257-260.
- PELLMYR, O. & J. N. THOMPSON., 1992.— Multiple occurrences of mutualism in the yucca moth lineage. *Proceedings of the National Academy of Sciences*, 89 : 2927-2929.
- PROUT, T., J. BUNDGAARD AND S. BRYANT., 1973.— Population genetics of modifiers of meiotic drive I. The solution of a special case and some general implications. *Theoretical Population Biology*, 4 : 446-465.
- RATNIEKS, F. L. W., 1993.— Egg-laying, egg-removal and ovary development by workers in queenright honey bee colonies. *Behavioral Ecology and Sociobiology*, 32 : 191-198.
- RATNIEKS, F. L. W. & H. K. REEVE., 1992.— Conflict in single-queen hymenopteran societies : the structure of conflict and processes that reduce conflict in advanced eusocial species. *Journal of Theoretical Biology*, 158 : 33-65.
- RATNIEKS, F. L. W. & P. K. VISSCHER., 1989.— Worker policing in the honeybee. *Nature*, 342 : 796-797.
- REEVES, H. K. & P. NONACS., 1992.— Social contracts in wasp societies. *Nature*, 359 : 823-825.
- REGAL, P. J., 1977.— Ecology and evolution of flowering plant dominance. *Science*, 196 : 622-629.
- REMY, W., T. N. TAYLOR, H. HASS & H. KERP., 1994.— Four hundred-million-year-old vesicular arbuscular mycorrhizae. *Proceedings of the National Academy of Sciences, USA*, 91 : 11841-11843.
- ROBINSON, G. E., 1992.— Regulation of division of labor in insect societies. *Annual Reviews of Entomology*, 37 : 637-665.
- ROBINSON, G. E. & R. E. PAGE JR., 1988.— Genetic determination of guarding and undertaking in honey-bee colonies. *Nature*, 333 : 356-358.
- ROBINSON, G. E., R. E. PAGE JR., C. STRAMBI & A. STRAMBI., 1989.— Hormonal and genetic control of behavioral integration in honey bee colonies. *Science*, 246 : 119-112.
- ROISIN, Y., 1994.— Intragroup conflicts and the evolution of sterile castes in termites. *American Naturalist*, 143 : 751-765.
- ROWAN, R. & N. KNOWLTON., 1995.— Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceedings of the National Academy of Sciences, USA*, in press.
- ROWAN, R. & D. A. POWERS., 1991.— A molecular genetic classification of zooxanthellae and the evolution of animal-algal symbioses. *Science*, 251 : 1348-1351.
- ROWELL, T. E., 1975.— Growing up in a monkey group. *Ethos*, 3 : 113-128.
- ROWELL, T. E., 1987.— On the significance of the concept of the harem when applied to animals. *Social Science Information*, 26 : 649-669.
- RUSSELL, J. K., 1982.— Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food resources. pp. 413-431 in E. G. LEIGH JR., A. S. RAND & D. M. WINDSOR, eds. *The*

- Ecology of a Tropical Forest*, Smithsonian Institution Press, Washington DC.
- SCHALLER, G. B., 1972.— *The Serengeti Lion*. University of Chicago Press, Chicago.
- SCHUPP, E. W., 1986.— *Azteca* protection of *Cecropia*: ant occupation benefits juvenile trees. *Ecologia*, 70: 379-385.
- SCHUPP, E. W. & D. H. FEENER Jr., 1991.— Phylogeny, lifeform, and habitat dependence of ant-defended plants in a Panamanian forest. pp. 177-197 in C. R. HUXLEY & D. F. CUTLER, eds. *Ant-Plant Interactions*. Oxford University Press, Oxford.
- SEELEY, T. D., 1989a.— The honey bee colony as a superorganism. *American Scientist*, 77: 546-553.
- SEELEY, T. D., 1989b.— Social foraging in honey bees: how nectar foragers assess their colony's nutritional status. *Behavioral Ecology and Sociobiology*, 24: 181-199.
- SEELEY, T. D., 1994.— Honey bee foragers as sensory units of their colonies. *Behavioral Ecology and Sociobiology*, 34: 51-62.
- SEELEY, T. D., S. CAMAZINE & J. SNEYD., 1991.— Collective decision-making in honey bees: how colonies choose among nectar sources. *Behavioral Ecology and Sociobiology*, 28: 277-290.
- SEELEY, T. D. & R. A. LEVIEN., 1987.— A colony of mind. *The Sciences*, 27: 28-43.
- SIMON, L., J. BOUSQUET, R. C. LÉVESQUE & M. LALONDE., 1993.— Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature*, 363: 67-69.
- SILVER, L. M., 1985.— Mouse *t* haplotypes. *Annual Review of Genetics*, 19: 179-208.
- SLATKIN, M. & M. J. WADE., 1978.— Group selection on a quantitative character. *Proceedings of the National Academy of Sciences, USA*, 75: 3531-3534.
- SMITH, A., 1759.— *The Theory of Moral Sentiments*. London, A. Millar.
- SMITH, A., 1776.— *An Enquiry into the Nature and Causes of the Wealth of Nations*. London, W. Strahan & T. Cadell.
- SMITH, W. J., 1986.— An "informational" perspective on manipulation. pp. 71-86 in R. W. MITCHELL & N. S. THOMPSON, eds. *Deception. Perspectives on Human and Nonhuman Deceit*. State University of New York Press, Albany.
- SMYTHE, N., 1977.— The function of mammalian alarm advertising: social signals or pursuit invitation? *American Naturalist*, 111: 191-194.
- SMYTHE, N., 1989.— Seed survival in the palm *Astrocaryum standleyanum*: evidence for dependence upon its seed dispersers. *Biotropica*, 21: 50-56.
- SUSSMAN, R. W., 1991.— Primate origins and the evolution of angiosperms. *American Journal of Primatology*, 23: 209-223.
- SZATHMARY, E. & L. DEMETER., 1987.— Group selection of early replicators and the origin of life. *Journal of Theoretical Biology*, 128: 463-486.
- SZATHMARY, E. & J. MAYNARD SMITH., 1995.— The major evolutionary transitions. *Nature*, 374: 227-232.
- TAYLOR, P. D. & M. G. BULMER., 1980.— Local mate competition and the sex ratio. *Journal of Theoretical Biology*, 86: 409-419.
- TERBORGH, J., 1986.— Keystone plant resources in the tropical forest. pp. 330-344 in M. E. Soulé, ed. *Conservation Biology*. Sinauer Associates, Sunderland, MA.
- THOMPSON, J. N., 1994.— *The Coevolutionary Process*. Chicago, University of Chicago Press.
- TIFFNEY, B. H., 1984.— Seed size, dispersal syndromes, and the rise of the angiosperms: evidence and hypothesis. *Annals of the Missouri Botanical Garden*, 71: 551-576.
- TRENCH, R. K., 1987.— Dinoflagellates in non-parasitic symbioses. pp. 530-570 in F. J. R. Taylor, ed. *The Biology of Dinoflagellates*. Oxford, Blackwell Scientific.
- TRIVERS, R. L. & H. HARE., 1976.— Haplodiploidy and the evolution of the social insects. *Science*, 191: 249-263.
- TURELLI, M., 1984.— Heritable genetic variation via mutation-selection balance: Lerch's zeta meets the abdominal bristle. *Theoretical Population Biology*, 25: 138-193.
- VON NEUMANN, J. & O. MORGENSTERN., 1944.— *Theory of Games and Economic Behavior*. Princeton University Press, Princeton NJ.
- WADE, M. J., 1978.— A critical review of the models of group selection. *Quarterly Review of Biology*, 53: 101-114.
- WERREN, J. H., U. NUR & C.-I. WU., 1988.— Selfish genetic elements. *Trends in Ecology and Evolution*, 3: 297-302.
- WEST, S. A. & E. A. HERRE., 1994.— The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig-pollinator mutualism. *Proceedings of the Royal Society of London B*, 258: 67-72.
- WEST-EBERHARD, M. J., 1979.— Sexual selection, social competition, and evolution. *Proceedings of the American Philosophical Society*, 123: 222-234.
- WEST-EBERHARD, M. J., 1981.— Intragroup selection and the evolution of insect societies. pp. 3-17 in R. D. ALEXANDER & D. W. TINKLE, eds. *Natural Selection and Social Behavior: Recent Research and New Theory*. Chiron Press, New York.
- WEST-EBERHARD, M. J., 1987.— Flexible strategy and social evolution. pp. 35-51 in Y. ITO, J. L. BROWN & J. KIKKAWA, eds. *Animal Societies: Theories and Facts*. Japan Science Society Press, Tokyo.
- WIEBES, J. T., 1979.— Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics*, 10: 1-12.
- WILLIAMS, G. C., 1979.— The question of adaptive sex ratio in outcrossed vertebrates. *Proceedings of the Royal Society of London, B*, 205: 567-580.
- WILLIS, E. O., 1967.— The Behavior of Bicolored Antbirds. *University of California Publications in Zoology*, 79: 1-132.
- WILSON, D. S., 1975.— A theory of group selection. *Proceedings of the National Academy of Sciences, USA*, 72: 143-146.
- WILSON, D. S., 1980.— *The Natural Selection of Populations and Communities*. Benjamin/Cummings, Menlo Park, CA.
- WINDSOR, D. M., D. W. MORRISON, M. A. ESTRIBI & B. DE LEON., 1989.— Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panamá. *Experientia*, 45: 647-653.
- WING, S. L., L. J. HICKEY & C. C. SWISHER., 1993.— Implications of an exceptional fossil flora for late Cretaceous vegetation. *Nature*, 363: 342-344.
- WRIGHT, S., 1951.— The genetical structure of populations. *Annals of Eugenics* (now *Annals of Human Genetics*), 15: 323-354.
- WU, C.-I. & M. F. HAMMER., 1991.— Molecular evolution of ultraselfish genes of meiotic drive systems. pp. 177-203 in R. K. SELANDER, A. G. CLARK & T. S. WHITTAM, eds. *Evolution at the Molecular Level*. Sinauer Associates, Sunderland, MA.
- ZEH, D. W. & J. A. ZEH., 1991.— Dispersal-generated sexual selection in a beetle-riding pseudoscorpion. *Behavioral Ecology and Sociobiology*, 30: 135-142.
- ZEH, D. W. & J. A. ZEH., 1992.— Emergence of a giant fly triggers phoretic dispersal in the neotropical pseudoscorpion, *Semeiochernes armiger* (Balzan) (Pseudoscorpionida: Chernetidae). *Bulletin of the British Arachnological Society*, 9: 43-46.
- ZEH, J. A. & D. W. ZEH., 1994.— Tropical liaisons on a beetle's back. *Natural History*, 103: 36-43.

- ZIMMERING, S., L. SANDLER & B. NICOLETTI., 1970.— Mechanisms of meiotic drive. *Annual Review of Genetics*, 4: 409-436.
- ZOTZ, G., G. HARRIS, M. KÖNIGER & K. WINTER., 1995.— High rates of photosynthesis in the tropical pioneer tree, *Ficus insipida* Willd. *Flora*, 190: 265-272.

VERSION FRANÇAISE ABRÉGÉE

Au cours de plusieurs périodes critiques de l'évolution du vivant, comme celle de l'émergence de l'endosymbiose des eucaryotes, celle de la coordination pour la reproduction sexuelle, de la duplication de plusieurs gènes en une méiose ordonnée, ou celles de l'évolution des organismes pluricellulaires et des groupes sociaux, des ensembles simples ont été regroupés en entités plus complexes. Ces ensembles nouveaux ne peuvent apparaître que si la sélection naturelle favorise des relations harmonieuses et une interdépendance à l'intérieur du groupe où les parties interagissent, de façon à transformer le groupement en un tout.

Dans quelles conditions la sélection naturelle peut-elle favoriser l'émergence de ces relations harmonieuses d'interdépendance ? S'il n'y a pas d'échange de migrants entre les groupes et si chaque groupe est composé d'individus issus d'un seul groupe parental — comme dans le cas des populations de mitochondries de différents protistes d'une même espèce — la sélection entre groupes est plus importante que la sélection à l'intérieur des groupes, et elle favorise les individus les plus utiles au groupe. Dans les groupes formés des jeunes issus de plusieurs parents, la compétition entre individus est favorable au groupe, à condition que ses membres puissent neutraliser les individus "hors la loi" qui entrent en compétition en utilisant des moyens nuisibles à l'ensemble du groupe. Ce principe s'applique aux gènes des chromosomes du génome, dans le cas de la reproduction sexuée. Dans ce cas, la sélection sur d'autres loci favorise les allèles qui suppriment la ségrégation/distorsion due aux mutants dont la méiose est biaisée en leur faveur. Il en résulte une méiose "équitable" permettant aux allèles de se répandre uniquement si l'individu

qui les porte en bénéficie. Enfin, les mammifères et les poissons qui forment des groupes sociaux leur permettant d'éviter la prédation doivent rester groupés pour éviter d'être pris individuellement : dans de tels groupes, un individu prend des risques s'il rompt l'homogénéité du groupe dont il dépend.

La sélection dans les groupes ou le contrôle mutuel qu'exercent entre eux les individus d'un groupe ne peut changer le groupe en une unité intégrale que s'il existe à la fois un intérêt commun à tous les membres — tel que la dépendance d'un parasite à la survie de son hôte ou le bénéfice que les membres d'une société d'insectes dérivent de la division des tâches — et des conditions permettant que cet intérêt commun reste prévalent parmi les membres du groupe. L'utilisation d'un hôte sous forme de territoire d'où les migrants de même espèce sont exclus a permis la sélection de groupe des mitochondries ancestrales qui, de parasites, sont devenues des organites. La reine des abeilles crée un intérêt commun des ouvrières à sa reproduction par le fait qu'il est désavantageux pour les ouvrières de pondre leurs propres œufs.

Les formes de mutualisme sont importantes et très généralisées dans les systèmes biologiques. Certaines de ces formes peuvent exister en dépit de l'absence de pression de sélection des groupes ou des mécanismes permettant de punir les "tricheurs". Les relations de mutualisme, telles que celles qui lient les plantes et les mycorhizes ou les coelentérés et les zooxanthellae, ont considérablement transformé les écosystèmes terrestres et marins. L'utilisation des animaux pour polliniser les fleurs ou disséminer les graines aboutit à une amélioration de la productivité, ainsi qu'à un recyclage rapide et bénéfique des éléments nutritifs des restes de végétaux dans les forêts d'angiospermes, en particulier dans les forêts tropicales. Les figuiers sauvages (*Ficus* spp.) ont abouti à un système de pollinisation extrêmement efficace par une forme de "domestication" des guêpes pollinisatrices, chaque espèce étant propre à une espèce de *Ficus*. Ces figuiers à croissance et enracinement très rapides, qui contribuent à une partie disproportionnée de l'alimentation des animaux de la forêt, sont un reflet du rôle autocatalytique joué par le mutualisme dans l'organisation et dans l'évolution des communautés dans les écosystèmes.